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The Neural Dynamics of Action Representation for Sound

An investigation of musical training effects on mu suppression

Che-Rong Carolyn Wu

Abstract
Efficient sensorimotor integration is essential for music performance. Musicians undergo extensive training, which enhances established neural links between auditory and motor areas of the brain. Long-term training develops, strengthens and enables flexibility in these connections allowing proficiency in performance. Functional neuroimaging studies have indicated that listening to trained music can result in the activity in premotor areas, even after a short period of training. This suggests that such mappings can be specific, and can rapidly become automatic. It has been argued that although these are abstract associations, these mappings rely on activity in mirror neuron systems (involved generally in imitating and learning actions). It has also been suggested that these systems are heavily dependent on actual sensorimotor experience; however others suggest that humans naturally move to music and therefore actual sensorimotor training is not necessary to demonstrate action representation during listening to music. Electroencephalography (EEG) studies in the action-observation field have associated changes in mu rhythm activity with the mirror neuron system for observation of actions as well as the more abstract association of observation of musical notation. The overall aims of this current thesis were to extend this visuomotor work into the audiomotor domain, and investigate whether specific sensorimotor training led to action representation for auditory stimuli.

Study 1 showed that sensorimotor mu rhythm desynchronisation occurred when pianists listened passively to piano melodies, demonstrating that this spectral analysis method can be used to detect action representation during listening. Study 2 sought to determine if similar action representation during passive listening occurs specifically for newly acquired sound-action mappings after short-term musical training. Somewhat unexpectedly, significant mu suppression was not revealed post-training, for either piano tone stimuli or rhythmic stimuli.
In Study 3 spectral coherence methods were used, and it was found that functional connectivity increased after musical training for specific listening tasks. This last finding suggests that there is some degree of specificity in the modulation of task-related coherence due to training, as the increased coherence did not occur for rhythmic stimuli. We consider possible explanations for these varied findings, and discuss the relevance of these studies to brain plasticity, sensorimotor integration and relatively recent developments in music-supported therapy for stroke rehabilitation.
Acknowledgements

“The Long and Winding Road” (The Beatles, 1970)

Many thanks to all who have helped and supported me along the journey of my graduate research years. There are too many wonderful and inspiring people to acknowledge here. From piano performance and pharmacology studies to neuroscience and psychology – the road has indeed been long and winding.

First and foremost, thank you to my supervisors: Professor Ian Kirk for his continuous support and encouragement, Professor Jeff Hamm for always being willing to step in and provide helpful insight when called upon, and Doctor Vanessa Lim for mentoring me from the very beginning of my studies in music neuroscience. I also thank Doctor Marc Bangert for allowing his adaptive training paradigm to be modified and used in this thesis.

However, there is one teacher that I wish to especially acknowledge, and that is Doctor Rae de Lisle: musician, pedagogue, and now rehabilitator extraordinaire. It was Rae’s piano tutelage, determination to succeed at rehabilitating focal dystonia musicians, and drive for the need for musicians’ health awareness and action that ultimately led me to the research field of music neuroscience, and also instilled in me a passion for teaching. Thank you Rae.

I would like to extend my appreciation to the willing participants involved in these studies - this thesis would not have been possible if it were not for each of them.

I am also grateful for the availability of the University of Auckland Doctoral Scholarship, which has partially funded this PhD.

Thanks to all those who I saw as student mentors when I arrived in the graduate lab: Doctors Reece Roberts, Nick McNair, Scott Fairhall, Branka Milivojevic, Suzanne Rolfe. I would like to express my special thanks to Doctor Sarina Iwabuchi for her amazing support throughout all our graduate years. Thanks also to my fellow students in the lab: Chris, Katharina, Haeme, Nicole, Kristina, Ashleigh and Bradley.

And a huge thank you to my family, for their unrelenting support.
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Chapter 1. Introduction

1.1 Musical Training and Neural Plasticity

Learning to play a musical instrument is a complex process that involves the acquisition of sensorimotor skills. In musical training, the development and refinement of neural connections between sensory and motor regions of the brain is crucial as successful music performance involves the ability to efficiently integrate motor, auditory, visual, and somatosensory modalities. Consequently, this suggests that musical training would be useful for the study of sensorimotor integration and functional plasticity in the brain (Münte, Altenmüller, & Jäncke, 2002; Pantev & Herholz, 2011; Zatorre, Chen, & Penhune, 2007).

Musicians undergo extensive musical instruction over a long period of time. Therefore, even though musicians do not make up a homogeneous population (e.g. in terms of skill level, training, age of commencement, intensity of training, instrument played), this particular group has been invaluable for investigating training effects. In cognitive neuroscience, training-related differences between musicians and non-musicians have been reported in neural structure and function, and in the behavioural consequences of these differences. Whether some of these differences are due to innate susceptibilities to training effects is a matter for speculation; yet there is consensus that musicians do indeed demonstrate differences in particular structures, including motor output areas as well as auditory cortices (Gaser & Schlaug, 2003). For example, the anterior corpus callosum of musicians who had begun training before the age of seven was reported to be larger relative to musicians who had commenced later, as well as to non-musicians (Schlaug, Jäncke, Huang, Staiger, & Steinmetz, 1995). In addition, keyboard players had more symmetrical motor hand representations in the cortex, as shown by the intrasulcal length of the precentral gyrus in magnetic resonance images, compared to controls (Amunts et al., 1997). This demonstrates
that finger representation is modified by musical training, and the typical asymmetry of particular areas of the cortex are less apparent in musicians. In this case, this could be attributed to evenness between the use of the hands, especially in music keyboard training.

However, it should not be concluded that music training is required in order to reach optimum capacity and structure in these particular areas of the brain - these structural changes are merely a striking example of the plasticity of the brain which responds to repeated stimulation, and is not limited to music training. Nevertheless musicians have been acknowledged as a useful population for understanding the potential and mechanisms of the plastic ability of the brain.

Evidence is also establishing functional changes associated with musical training. Functional imaging studies have also found changes in finger representation, for example, magnetoencephalography (MEG) recorded during tactile stimulation revealed that left-hand digits of string players had greater representation in the cortex than in non-musician controls (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995). Musicians also showed greater strength in auditory cortical activation at the N1m component (the MEG counterpart of N1) when hearing piano tones compared to pure tones (Pantev et al., 1998). Timbre-specific plasticity has also been demonstrated with violinists showing greater auditory cortical strength for violin tones compared to trumpet tones and trumpeters showing the opposite pattern (Pantev, Roberts, Schulz, Engelien, & Ross, 2001). This timbre effect has also been studied using electroencephalography (EEG), where musicians showed greater induced gamma band activity over auditory regions for listening to tones of their specific instrument of expertise (violin or piano), and greater overall gamma band activity compared to non-musicians (Shahin, Roberts, Chau, Trainor, & Miller, 2008). Margulis and colleagues (2009) demonstrated a similar timbre-specific plasticity effect using functional magnetic resonance
imaging (fMRI). They reported greater activation for their instrument of expertise (violin or flute) in a network of regions including IFG, precentral gyrus, and STG.

Comparisons between amateur and professional musicians have shown effects of the level of expertise. Amateur musicians demonstrated more widely distributed activation in sensorimotor cortex and cerebellum, greater prefrontal and basal ganglia activation and less auditory activation than professional violinists during execution of finger movements and imagination of a violin concerto (Lotze, Scheler, Tan, Braun, & Birbaumer, 2003). The authors suggest that this is indicative of automation of movements in professionals, with less activation of associated motor programming areas than amateurs. They also note that differences in the auditory regions suggest an increased strength in auditory-motor connections in the professional musicians (Lotze et al., 2003). Another study revealed that professional pianists, due to being highly-practised, recruit less of the motor cortex during tapping tasks, which, although contrasting the evident structural increase in hand representation of cortex, shows that long-term training results in a greater network of neurons involved in motor control of the hand but allows for improved functional efficiency (Jäncke, Shah, & Peters, 2000). It seems that reports of greater recruitment of certain areas during training are also accompanied in the literature by the somewhat paradoxical reduction in activation in professionals, which could suggest that one may become more efficient as one becomes expert.

To date, apart from the above studies on timbre-specificity effects for listening to tone stimuli, research on the effects of instrument-specificity has been left somewhat under-addressed in studies that include a motor component. This is not surprising, as equating two groups who have been trained on different instruments is no easy task. There is also the potential for additional confounds due to the different motor skills required for different instruments, and many musicians train in more than one instrument. One recent study that did
investigate instrument specificity of sensorimotor systems has shown coactivation of the auditory cortex specifically for trumpet players but not pianists during silent fingering movements on a MRI-compatible trumpet (Gebel, Braun, Kaza, Altenmüller, & Lotze, 2013). However, most studies focus on piano keyboard (e.g. Baumann et al., 2007), although some recruit other instrumentalists, such as violinists (Elbert et al., 1995; Kajihara, Verdonschot, Sparks, & Stewart, 2013; Lotze et al., 2003).

In addition, within these already limited categories, most studies employ unimanual tasks unless the task is generic, such as finger tapping (Jäncke et al., 2000). Therefore hemispheric lateralisation in relation this topic has also, as yet, gone largely unaddressed. Studies of sensorimotor integration with musicians and musical training cannot yet elucidate lateralisation effects as studies to date have only trained one effector. One study did include both right and left hand actions on a piano keyboard (a Mozart sonata (K.545) and scales; Baumann et al., 2007), although laterality was not addressed by the authors.

Similarly, violin studies have mainly concentrated on the left hand, and therefore these studies do not, and possibly cannot, address the issue of laterality either, because the roles of each hand are so different in violin playing (Elbert et al., 1995; Lotze et al., 2003). It may seem obvious that piano players may be a more suitable group for studying laterality effects as pianists aim to be highly skilled and equal in strength, suppleness, and dexterity between the hands. Indeed, an advantage for piano sight reading has been shown by those who demonstrated reduced laterality in tapping ability between the hands (Kopiez, Galley, & Lee, 2006). However, even for a keyboard instrument, it is difficult to equate the hands, and one study noted that there is a higher number of notes and melodies played by the right hand in piano music, which may result in a right hand bias (regardless of handedness) due to the more extensive practice required of the right hand compared to the left over the many years of training (Kopiez et al., 2012). Furthermore, lateralisation effects may vary between studies
because experimental parameters of tasks, such as modality and complexity, may affect results. Laterality is clearly a topic of interest and worth discussing with regard to musical training, but it is also worth noting that caution must be taken when interpreting hemispheric lateralisation effects.

So far, the studies mentioned above demonstrate structural and functional changes in the brain due to musical training experience. It is also possible to explore changes in sensorimotor integration by investigating the strengthening of sensorimotor coupling that occurs through practice.

1.2 Sensorimotor Integration – The Importance in Translating Perception to Action

Perception-action coupling, which is enhanced through musical training, has been investigated in studies of professional pianists using interference task paradigms. Audiomotor representations were shown in pianists who had slower reaction times when playing an observed chord that was simultaneously presented with an incongruent auditory stimulus (Drost, Rieger, Brass, Gunter, & Prinz, 2005a). Similarly, hearing incongruent musical intervals affected the performance of a musical score (Drost, Rieger, Brass, Gunter, & Prinz, 2005b). Furthermore, hearing task-irrelevant musical scales interfered with performance in movement tasks, so that response time was quicker when the scale direction matched the required direction of movement (Taylor & Witt, 2014). Interestingly, Kajihara and colleagues (2013) argue that the interference effects reported by such studies could be a result of the horizontal spatial mapping of pitch (e.g. Spatial Musical Association of Response Codes (SMARC) effect; Rusconi, Kwan, Giordano, Umiltà, & Butterworth, 2006) that pianists acquire through training, rather than audiomotor mappings per se. However, even if the SMARC effect accounted for part of the effects found by the above studies, interference of
incongruent task-irrelevant auditory stimuli also occurs for violinists, when assuming a violin holding position, where spatial compatibility for horizontal pitch mapping is not so apparent (Kajihara et al., 2013). Overall, these studies provide support for the concept that training leads to the formation of audiomotor representations.

Musicians will often feel that the appropriate finger movements are triggered when listening to a musical piece they have played before. This phenomenon has also been demonstrated empirically in a MEG study where pianists showed involuntary movement of the fingers, represented by contralateral motor cortex activation during listening to learned music. Using brain surface current density reconstructions in order to localise activity, Haueisen and Knösche (2001) discovered spatially dissociated points of activation when pianists were listening to notes played by the thumb compared to notes played by the little finger, and this correlated to the locality of the motor homunculus (Haueisen & Knösche, 2001). Interestingly, activation in other motor areas known to be involved in motor programming was not detected. This is perhaps in accord with a study mentioned in the previous section (Jäncke et al., 2000), in which the authors proposed that training leads to an efficient network, and therefore expert musicians may not require recruitment of motor association areas. However, Haueisen and Knösche (2001) also highlight a technical limitation of MEG, which cannot localise activity to the supplementary motor area (SMA) due to the inability to detect magnetic activity in midline structures. Therefore, it is not fully elucidated as to whether activation in motor association regions occurred.

Other neuroimaging methods have been used to examine audiomotor representations. fMRI was employed to compare pianists to non-musicians while they passively listened to melodies and silently played on a piano keyboard (Bangert et al., 2006). A conjunction analysis revealed activation in regions involved in both tasks. This included a fronto-temporal network in only the pianist group, which demonstrates the close interaction between
perception and action for those trained in music. Fronto-parieto-temporal activation was also reported in another fMRI study when pianists heard melodies, again demonstrating action-perception coupling (Haslinger et al., 2005).

Using transcranial magnetic stimulation (TMS), increased motor excitability was shown in the right primary motor cortex of pianists listening to the left-hand line of a piece that was rehearsed before the experiment (D’Ausilio, Altenmüller, Belardinelli, & Lotze, 2006). These researchers posited that the audiomotor mapping only occurred if the specific movement had been performed, as the motor excitability increase was not found when listening to a flute piece in similar style to the rehearsed piano piece (D’Ausilio et al., 2006).

Perception-action literature on musicians, as mentioned above, has established that long-term music practice undoubtedly leads to structural and functional changes in the brain. Modulation of structure and function has also been revealed after a much shorter period of musical training. This has been demonstrated in studies of non-musicians1 who underwent training on a piano keyboard. These musical training studies were based on research that revealed brain plasticity occurring from short-term (non-music) training exercises consisting of simple finger movements (Classen, Liepert, Wise, Hallett, & Cohen, 1998).

Various neuroimaging methods have also been utilised to reveal brain plasticity after short-term training. Transcranial magnetic stimulation (TMS) mapping revealed hand-specific increased excitability of cortical motor areas during and after five days of piano exercises (Pascual-Leone, 2001). Bangert and Altenmüller (2003) measured event-related direct voltage EEG to study audiomotor integration after training. Participants used

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1 The term ‘non-musician’ is perhaps somewhat misleading as the majority of us have been exposed to music, and enjoy music. This topic is of great interest and importance in the field of music neuroscience but is beyond the scope of this thesis. Here, we use the term for those who have not had musical training and performance experience.
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interactive training software to learn to play melodies accurately up to a certain level that they heard on a piano keyboard, and during playing they received online auditory feedback. This five week training paradigm was designed to encourage auditory and motor binding, for specific sound-action mappings. EEG measurements were acquired before and after the first training session, before the sixth and before the eleventh 20 minute training sessions. These EEG recording sessions presented motor and auditory components in separate conditions, in order to investigate changes in the involuntary coactivation of the other modality after training. During passive auditory listening there was a shift from frontal and central activation found pre-training, to widespread activation that after ten sessions became more focal at left primary sensorimotor cortex regions. During silent movement, activity was initially centred on contralateral M1, then after initial training sessions included reduced activity in ipsilateral motor regions. After ten sessions, fronto-temporal regions also became active. In other words, motor coactivation occurred during the auditory task and auditory coactivation occurred during the motor task. No significant post-training differences were found for an additional training group for whom the piano notes presented in training trials were randomly switched between the keys so that no sound-action mapping could develop. Therefore, the significant functional changes after training found in the ‘map’ group could not be attributed to repetitive exposure to sounds and to the pressing of keys over the training period. Taken together, these findings suggest that sensorimotor coupling can easily be acquired through a short amount of training.

The implications of sensorimotor integration are addressed from a different angle in an MEG study which compared unimodal and multimodal musical training of a tone sequence (Lappe, Herholz, Trainor, & Pantev, 2008). This study clearly demonstrated the enhancement of MMNm responses in non-musicians, after learning to play a musical sequence, which were even greater than the heightened responses demonstrated by non-musicians who received
only auditory training of the same sequence (Lappe et al., 2008). As both groups were exposed to similar auditory stimuli through the training, this finding demonstrates that the multimodality of training was more effective than unimodal learning.

The above short-term training studies test groups of participants during at least two time points. This longitudinal approach provides an advantage over the cross-sectional studies that compare musicians to non-musicians. The direct comparison of musicians with non-musicians is problematic. There may be a multitude of underlying reasons why musicians are musicians and non-musicians are not musicians and purely sensorimotor training effects might easily be obscured in group comparisons. Moreover, if a task requires both groups to play an instrument, non-musicians may not be carrying out the same task as musicians and accuracy will differ between groups. For example, one study asked musicians to play a Mozart sonata on a plastic board, and non-musicians were instructed to tap complex finger movements on the plastic board as they were incapable of performing the same task (Baumann et al., 2007). However, surprisingly both groups demonstrated audiomotor coupling effects. This study did reveal differences between the groups when both had to imagine the movements that would produce the Mozart sonata – perhaps another task that non-musicians were incapable of performing (although it could be argued that some non-musicians rather convincingly play air guitar!). Interestingly, both musician and non-musician groups in this study became familiar enough to sing the auditory stimuli that comprised of the Mozart sonata and scales (Baumann et al., 2007). Non-musicians also briefly learned to play the scale sequence immediately before testing and the authors suggest that this may have been sufficient training to explain the audiomotor coupling effects non-musicians showed during silent tapping. In addition, singing the melody involves a vocal motor act to produce the desired sound. This study presents an interesting issue of the potential importance of specific muscles that produce the appropriate action for the sound.
Both groups were able to use the vocal tract to produce the sound, but only musicians could link a manual effector being associated with playing the sound. Given that musicians and non-musicians had similar activity in crossmodal networks during scale listening and playing suggests that simple sequence learning of a very brief time period is sufficient to associate the sound to the action.

1.3 Auditory Mirror Neurons and Audiomotor Integration

The research outlined above demonstrates that perception and action are indisputably linked during music training and performance. However the nature of the link between the two is still debated in the literature. One area of the research regarding perception-action representation has stemmed from non-human studies in rhesus monkeys (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Premotor neurons were found to fire not only during action but during mere observation of action, and furthermore, some of these neurons were active even when the end of the movement was hidden as long as the monkey knew the end result (Rizzolatti, Fadiga, Gallese, et al., 1996; Umiltà et al., 2001). These neurons were termed mirror neurons by the researchers, and were thought to be essential for action-understanding. Since then interest has escalated, especially for investigating human mirror neurons using indirect methods, which has been aided by the increasingly improved imaging techniques available.

One of the first studies to demonstrate the mirror neuron effect in humans used TMS to reveal that motor evoked potentials (MEPs) increased during observation of action, and crucially, the effect was shown in the muscles that would carry out the action observed (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Since then, the majority of studies still investigate the visual modality and its relation to action (Rizzolatti & Craighero, 2004). In contrast, audiomotor integration research with respect to mirror neuron hypotheses and
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methodology is scarce compared to these visuomotor studies. An indication of the emphasis that has been placed on the visual domain is illustrated by two recent large-scale meta-analyses on the neural network of regions involved in action observation and execution, or imitation: one covers only visuomotor studies (Caspers, Zilles, Laird, & Eickhoff, 2010); and another includes a subset of 12 auditory studies out of 125 studies (Molenberghs, Cunnington, & Mattingley, 2012). The auditory system plays a vital role in music performance and despite the lack of research involving the auditory domain, there is consensus among researchers that audiomotor integration networks do exist and it is crucial that auditory and motor systems become tightly coupled during musical training (Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Pa & Hickok, 2008).

Evidence for auditory and audiovisual mirror neurons in macaque monkeys has been documented in the literature. Tearing sounds or the sound of a dropped stick activated 13% of neurons in ventral premotor cortex which were involved in the performance of the equivalent hand action (Kohler et al., 2002). Interestingly, during non-action related sounds this response was not found. These findings were supported by an additional study which demonstrated that these neurons had differing degrees of specificity, as some neurons discharged more for actions the monkeys had greater experience with (Keysers et al., 2003).

In humans, one area of research that has investigated auditory perception and its relation to actions is speech. Auditory regions are recruited during syllabic articulation when the actual sound is masked (Paus, Perry, Zatorre, Worsley, & Evans, 1996). Conversely, action-related sentences activated a left fronto-parieto-temporal network incorporating Broca’s area in an fMRI study, which did not occur for syntactically equivalent non-action-related sentences (Tettamanti et al., 2005). These examples provide evidence for a motor theory of perception, which, in brief, postulates that perception of speech is directly related to the articulatory gestures involved in the production of speech sounds, rather than mapping with
acoustical properties of phonemes (see Liberman & Mattingly, 1985). The representation of speech, gestures, and speech production in Broca’s area could be one part of the system that allows for action execution-observation (Nishitani, Schurmann, Amunts, & Hari, 2005).

Auditory mirror neuron research in speech science has been extended to the investigation of auditory and motor representation of non-speech sounds. Action-related sound processing (e.g. hand clapping) has been compared to non-action-related sounds (e.g. a jug boiling water) in an event related potential (ERP) source localisation study, which determined that left posterior superior temporal and premotor areas were selectively activated only for the action-related sounds (Pizzamiglio et al., 2005). Similarly, auditory mirror neurons have been studied indirectly in musical performance research (Lahav, Saltzman, & Schlaug, 2007) – thus positing a broader involvement of these motor association areas rather than just for speech. In particular, Broca’s area, classically a language function area, has mirror neurons that are involved in perception of non-speech stimuli (Lahav et al., 2007; Pizzamiglio et al., 2005). Furthermore, this region and its right homologue are now suggested to have more generalised functions rather than purely having an important role in speech and language.

Lahav and colleagues (2007) demonstrated that music training can be invaluable in the study of audiomotor integration and mirror neurons. Participants with no previous formal music training learned to play a short piece of music with the right hand. FMRI revealed that after training, areas of a fronto-parietal motor network were activated during passive listening of extracts of the same musical piece (Lahav et al., 2007). Two other conditions in this experiment strengthened their hypothesis that the audiomotor integration was specific for trained sound-action mappings; passive listening to a second piece consisting of the same note range but differently ordered also showed some, but less, activity in motor regions and passive listening to extracts from a piece containing a different range of notes to the trained piece did not activate the motor network (Lahav et al., 2007). Furthermore, this included the
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IFG incorporating Broca’s area and the right hemisphere homologue. Differentiation in left IFG activity across the three conditions was highlighted by the researchers as evidence for this region’s involvement in the auditory mirror neuron system (Lahav et al., 2007). These newly-acquired networks are purportedly made by the tuning of auditory mirror neurons to specific audiomotor mappings.

Thus, it is becoming more established that music and musical training can be useful for elucidating further the extent and functions of auditory mirror neuron systems. Lahav and colleagues (2007) used fMRI to determine if audiomotor activation occurred in brain regions that are suggested to be areas with auditory mirror neurons. Another approach utilised to study the role of the mirror neuron systems in sensorimotor coupling is to investigate the modulation of mu rhythm from electrophysiological recordings of oscillatory activity.

1.4 Mu Rhythm and the Mirror Neuron System

The mu rhythm may play an important role in linking perception and action, and has been proposed to represent a mechanism by which perception and action share a representation. The mu frequency band was first thought to represent ‘idling state’ as it was recorded over human sensorimotor cortex in the absence of motor output or sensory processing (Pineda, 2005). Furthermore, these 8-12 Hz rhythms were originally thought to be recordable from only few participants (McFarland, Miner, Vaughan, & Wolpaw, 2000). However, it is now known that most adults have mu rhythm and evidence of mu rhythm suppression during cognitive function has led to much research focussing on elucidating the exact relationship between this rhythm and cognitive processing (McFarland et al., 2000; Obermann, Pineda, & Ramachandran, 2007). There are slight discrepancies in the range of mu (e.g. 7 to 14 Hz; Pfurtscheller, Neuper, & Krausz, 2000), and in addition to an alpha frequency range band, it is reported that mu rhythm also has a beta frequency range (~20 Hz).
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 (~20 Hz; Hari, 2006). These two frequency bands have been shown to be related, but demonstrate various differing properties. For example, the topography of the alpha and beta differs, and there is also evidence of independent processes (McFarland et al., 2000). Beta band oscillations might be involved in sensorimotor integration through monitoring and recalibration of motor output, and have been found to be suppressed by movement or motor imagery (Baker, 2007; Pfurtscheller, Neuper, Brunner, & da Silva, 2005). This suggests that rather than having a functional role in the actual movement per se, they are involved in monitoring of the movements and preparation for following movements (Baker, 2007).

Evidence is now accumulating to suggest that mu suppression indicates mirror neuron system activity. In an action-observation study, mu rhythm attenuated during observation, imitation, and execution of hand grip actions (Muthukumaraswamy & Johnson, 2004a). This study was extended to show that mu desynchronisation appeared to be a sensitive index for properties of the mirror neuron system, such as greater mu attenuation occurring during observation of a goal-directed movement than observation of a non-goal-directed movement (Muthukumaraswamy, Johnson, & McNair, 2004).

Further support for the mu rhythm being involved in mirror neuron systems has come from a combination of other neuroimaging methods. Mu suppression was related to an increase in blood oxygen level dependent (BOLD) signal in human mirror neuron system regions: dorsal premotor cortex, inferior parietal lobe, posterior somatosensory cortex, and (weaker) in ventral premotor cortex in action observation and execution tasks (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011). Furthermore, applying TMS to the IFG abolished the mu suppression over sensorimotor cortex in the 8-12 Hz range during observation of movement videos (Keuken et al., 2011). The anatomical location of mu suppression supports the hypothesis that this particular band of oscillations relates to mirror neuron activity as
there are strong connections between ventral premotor cortex and primary sensorimotor cortex (Obermann et al., 2007).

Auditory mirror neuron research documented in the previous section highlights a possible laterised effect, which has led to suggestions of a gesture basis of language, and is in contrast to the bilateral suppression revealed by action-observation studies (Paus et al., 1996; Tettamanti et al., 2005; Zatorre et al., 2007). Pineda and colleagues (2013) reported that action-related sounds produced mu suppression effects in the left hemisphere of participants, while non-action sounds revealed mu suppression over the right hemisphere. They discuss that the environmental sounds used as non-action stimuli could still be somewhat associated with motor systems (for example, an individual could still experience embodiment of some action that is associated with the event of a train rushing past). Again, these findings suggest that there is specificity in the way the mirror neuron system responds to varying stimuli.

Mu suppression has also been investigated for musical stimuli, and a study reported that both musicians and non-musicians showed mu desynchronisation when watching videos of musical performances, however, only musicians demonstrated mu suppression during musical score reading (Behmer Jr. & Jantzen, 2011). These findings suggest that mu suppression can occur for abstract associations between music notation and actions that have formed by musical training.

These electrophysiological and anatomical studies together provide sufficient evidence to show the role of mu suppression in human mirror neuron systems and action representation during observation and listening. Therefore, mu rhythms may be useful in revealing certain properties of the sensorimotor integration and auditory mirror neuron system, such as how specifically this system responds.
1.5 Mu Rhythm = Mu-sical Rhythm?

One aspect of auditory mirror neuron system specificity is currently under debate in the music perception and action field. The phenomenon of wanting to tap to the beat when hearing rhythmic sounds is commonly experienced, and has prompted researchers to ask whether the presence of a metrical beat is sufficient enough to activate the audiomotor network. According to Chen, Zatorre and Penhune (2006), because we regularly tap to the beat when listening to music, the motor network including dorsal premotor areas is activated whenever there is a metrical salient beat. This would suggest that the sensorimotor integration system responds broadly, and specific sound-action mappings or experience of producing appropriate actions for specific sounds may not be necessary to reveal mu rhythm attenuation effects during sensorimotor processing.

However, in contradiction to the above view, a TMS study reported that motor excitability increased only when pianists listened to a rehearsed keyboard piece, and not when they listened to a flute piece (D’Ausilio et al., 2006). The specificity of findings from another aforementioned study also suggests that experience is crucial to demonstrate action representation, as learning to play a melody led to an audiomotor response only for that particular melody and not similar melodies (Lahav et al., 2007). Furthermore, another training study compared audio-visual-motor training to audio-visual training, and found that enhanced MMNm to audio-visual stimuli after training only occurred when training incorporated the motor experience (Paraskevopoulos, Kuchenbuch, Herholz, & Pantev, 2012). These studies appear to suggest that acquiring specific sound-action mappings may be crucial, and that hearing a rhythmic sequence may not activate the auditory mirror neuron system unless one has had audiomotor training.
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However, Chen, Penhune and Zatorre (2008) provided further support for a broader, less specialised action representation system. To distinguish between motor response to purely passive listening to rhythms, and listening when expected to subsequently synchronise movements to rhythms, Chen and colleagues (2008) contrasted a naïve passive listening condition to one where participants were instructed to anticipate the task of tapping to the rhythms after hearing them. They reported that similar motor regions were activated for both tasks, suggesting that everyone has an inherent action-perception coupling that is active when listening to music. However, the ventral premotor cortex was only active when participants anticipated that they would have to tap to the rhythm, and they suggest that this region does map sounds to actions specifically, whereas other premotor regions are activated regardless of whether there is anticipation to move to the music (Chen et al., 2008).

Given the above evidence of the utility of using mu rhythm as an index of mirror neuron activity, mu rhythm attenuation effects may reveal potential differences between auditory stimuli with different properties. Mu suppression may demonstrate action representation to sounds that one knows the appropriate movements for, in sensorimotor repertoire. Also, perhaps mu suppression may be revealed for any rhythmic sound, contributing to this debate.

1.6 The Musical Imagination and Terminology

There is another issue which is emerging from the body of work investigating sensorimotor processes and auditory mirror neuron systems in relation to action representation for music that must be addressed. The contribution of music imagery to the audiomotor process may be regarded as a potential confound, or separate process in this area of research. However, task instructions used in studies sometimes incorporate a perceptual task that is carried out during the listening, and if imagery still occurs, researchers argue that it is nevertheless an involuntary process (Haueisen & Knösche, 2001; Lotze et al., 2003).
address the issue of music imagery affecting audiomotor activation, one study contrasted a listening task where explicit instructions were given to imagine playing the music (voluntary), to a listening task where participants had to perform a visual distractor task (involuntary; Baumann et al., 2007). Activity increased in audiomotor network regions during voluntary imagery, and increased in fewer regions during the involuntary condition. The researchers suggest that perhaps imagery and action representation are not separate processes, but should be investigated separately (Baumann et al., 2007). This study highlights a discrepancy in the literature in terminology. Here, involuntary action representation occurs when participants are attending to a non-auditory stimulus. Furthermore, introducing an extra task that is not related to the auditory stimulus results in unequal attention toward the auditory stimuli between tasks. The lack of activation in the involuntary condition could be partly due to this. Perhaps then, the involuntary studies that still require listening to the stimulus in order to carry out the distractor task are the most appropriate – studies that include, for example, auditory discrimination tasks.

Similarly, another term requires close attention to how it is defined. Brown and Martinez (2007) argue that during passive listening, the primary and secondary auditory areas are activated, and premotor activation only occurs when the task asks for a discrimination judgement to be made. In their study they specifically focussed on vocal planning as part of a melody/harmony discrimination strategy, and distinguished discrimination and passive listening as separate types of tasks. This approach may appear to be a contradiction of the interpretation of the findings of studies that investigate passive listening and audiomotor activation (e.g. Bangert & Altenmüller, 2003; Haueisen & Knösche, 2001; Lahav et al., 2007 previously described). However, it might be argued that passive listening in the latter studies would be comparable to the discrimination tasks in Brown and Martinez (2007), and the only contradiction lies in the differing definitions of ‘passive’ task. In a mu suppression study,
participants were required to detect oddball events that were randomly interspersed during the experiment, in order to ensure *active* listening to the stimuli (Pineda et al., 2013). Again, there is a discrepancy in defining the type of listening task, as active listening in Pineda et al.’s (2013) study is comparable to passive listening in other studies (Lahav et al., 2007).

Despite the discrepancies in definitions and interpretations, all studies point in the same direction – researchers aim to evoke *involuntary* motor activation, as opposed to voluntary activation, but most do require participants to be attentive to the music they are listening to. Therefore one must take caution when defining the term ‘passive listening’ in experiments. Participants do not move voluntarily and therefore it is not active listening, but it is not passive per se because participants are required to attend to the stimulus and sometimes perform a task afterwards in order to ensure attentiveness. For lack of a better term, the term ‘passive’ is used to simply highlight there being no explicit movement.

Lotze and colleagues (2003) postulate tight coupling between primary motor and primary auditory areas only during executed activities because no primary auditory cortex activation was found during an imagery task despite participants reporting ‘high imagery vividness’. In constrast, Hickok and colleagues (2003) acknowledge that activation of the posterior dorsal superior temporal gyrus during a task where participants listened to previously rehearsed sentences or music is to do with auditory imagery. They instead explain that the auditory-motor integration after rehearsal in fact, enhances the auditory imagery process (Hickok et al., 2003). On a similar note, it has already been suggested that neurons involved in imagining conditions may hold mirror neuron properties (Kristeva, Chakarov, Schulte-Mönting, & Spreer, 2003).

Although frontal motor regions are discussed in auditory mirror neuron research, one would expect other motor association areas involved in the proposed motor representation
system to show involvement in the audiomotor integration process as well, such as posterior parietal regions – regions known to be involved in imagined movement (Pa & Hickok, 2008). Interestingly a structural connectivity study revealed posterior superior temporal regions connected to Broca’s area, not only through the classical arcuate fasciculus fibres but also a pathway projecting through the inferior parietal region (Catani, Jones, & ffytche, 2005). These results suggest that in audiomotor integration, networks are complex and may be utilised during imagery.

In a review on auditory-motor interactions, imagery is suggested to have some role in audiomotor coactivation as shown by recruitment of premotor regions during listening, but this review notes that there are also cases where imagery alone cannot explain all and therefore it is not crucial for motor activation (Zatorre et al., 2007). Furthermore, a study reported that mental practice of the same exercises was enough to produce a decrease in activation threshold, again suggesting that imagery does play a role in audiomotor processes (Pascual-Leone, 2001). Given the complex nature of studying action representation, it would seem that imagery is an important aspect of the process, and research on both ‘involuntary’ and ‘voluntary’ processes will extend knowledge of sensorimotor systems, as long as they are clearly defined.

1.7 Connectivity in the Audiomotor Network and the Effects of Musical Training – A Potential for Clinical Applications

Collectively, the studies mentioned in previous sections show that musical training leads to associations between auditory and motor regions, and that sensorimotor integration may be related to human mirror neuron systems in an action-understanding type of process. One method of investigating coupling between regions is examining oscillatory coherence using electrophysiological measures.
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The linear dependency between oscillatory signals can be examined to study cortico-cortico functional connectivity (Gerloff, Braun, & Hallett, 2003). Brain regions that co-operate during a task demonstrate high coherence, particularly in alpha (8-12 Hz) and beta bands (13-30 Hz) for sensorimotor tasks (Andres & Gerloff, 1999; Andrew & Pfurtscheller, 1996). Tracking tasks are an example of such tasks that require sensorimotor integration. Visuomotor tracking tasks have demonstrated the involvement of beta band for sensorimotor integration, as greater coherence in this frequency range was found between central and occipital electrodes during tracking tasks which required integration of visual perception and motor behaviour when compared to tracking a visual stimulus without the need to adjust motor behaviour, or producing similar movements without tracking the visual stimulus (Classen, Gerloff, Honda, & Hallett, 1998). Similarly, modulation of oscillatory coupling has been investigated using short-term training that aims to improve sensorimotor tracking skill (Blum, Lutz, & Jäncke, 2007). Thus, coherence analysis can be another approach for investigating the formation and strengthening of sensorimotor associations due to musical training.

Training effects have also been studied to elucidate the potential efficacy of a type of sensorimotor rehabilitation for stroke patients that incorporates musical training (Altenmüller, Marco-Pallares, Münte, & Schneider, 2009). In contrast to current therapies that focus on the motor impairment by training regimes that include repeatedly making movements, music-supported therapy incorporates a sensorimotor training approach, and aims to improve functional connectivity between sensory and motor regions of the brain (Schneider, Münte, Rodriguez-Fornells, Sailer, & Altenmüller, 2010; Schneider, Schönle, Altenmüller, & Münte, 2007). One study reported increased beta coherence after music-supported therapy in a group of stroke patients, during the audiomotor tasks (playing a piano keyboard or drum pad) from training (Altenmüller et al., 2009). This is a relatively new and exciting field with further
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studies being carried out to gain more insight into potential effectiveness of therapy that incorporates a sensorimotor component (Altenmüller & Schlaug, 2013). Therefore, combining electrophysiological methods of regional oscillatory activity and oscillatory coupling between regions could provide a useful measure for studying the effectiveness of rehabilitation techniques.

1.8 Thesis Rationale

The current thesis aimed to use EEG methods to investigate brain plasticity, and in particular audiomotor integration, that occurs due to musical training. I endeavour to bring together research on multimodal processes involved during musical training with brain imaging techniques from mirror neuron research. To integrate from these fields of research, I investigated action representation for musical sounds by examining modulations of the EEG mu rhythm during passive listening tasks.

Firstly, as an index for action representation, mu rhythm attenuation was studied in highly skilled musicians to determine if this method was able to detect audiomotor system activity. Mu suppression has been investigated previously in visuomotor and audiovisual musical tasks (Behmer Jr. & Jantzen, 2011), and I aimed to extend the findings to the audiomotor domain.

Secondly, short-term musical training effects on mu rhythm modulation during action-listening processes were investigated. Non-musicians underwent musical training that aimed to create specific sound-action mappings. This study sought to examine the specificity of the action representation. According to previous literature, experience of specific sound-action associations is required (e.g. Lahav et al., 2007), but alternatively, because humans move to music regardless of musical training experience, any rhythmic stimulus could result in the occurrence of action representation (e.g. Chen, Penhune, & Zatorre, 2009). To investigate
these opposing views, mu rhythm power was compared between auditory tasks (relative to baseline) that consisted of listening to notes from training, new notes, and listening to rhythmic stimuli.

Thirdly, the effects of training on functional connectivity were investigated using EEG coherence measures. This study set out to determine if the sensorimotor cortex and other regions show increased functional connectivity after audiomotor training on the piano. Learning to play a musical instrument requires integration between sensory and motor processes, and modulations in functional connectivity due to musical training can examined using oscillatory measures. Again, it was of interest to compare different types of stimuli to demonstrate how specific any training effects were on connectivity effects.

Overall, the current thesis aims to extend research on sensorimotor integration that occurs during musical training, and provide insight into the specificity of the audiomotor system in action representation networks. Musical training processes and musicians are useful models for investigating brain plasticity processes, and these models have the potential to provide invaluable insight for clinical rehabilitation.
Chapter 2. Action Representation in Pianists

2.1 Introduction

Musicians undertake extensive training that involves the interaction between multiple modalities. Training develops associations between sounds and the motor acts that are required to create the sound. Musicians become highly skilled at performing accurate actions to produce desired tones, and can conversely translate these sounds into a sequence of appropriate actions. This is the result of musicians acquiring action representations for musical sounds. Listening to a piece of music can often trigger the actions involuntarily in musicians – once action-understanding is achieved, coactivation occurs in the sensorimotor system because action and effect are so closely coupled together.

The associations humans learn to make between sensory stimuli and actions, such as those encountered during musical training, are hypothesised to involve mapping by the human mirror neuron system (Behmer Jr. & Jantzen, 2011). This idea stems from single-cell studies in monkeys that demonstrated firing of specific subpopulations of premotor and parietal neurons during both action observation and the performance of similar actions (Rizzolatti & Craighero, 2004). Numerous studies have endeavoured to determine if the same mirror neuron phenomenon exists in humans. Using functional brain imaging methods such as PET, regions homologous to those where mirror neurons are found in experimental animals have been shown to activate during the performance and observation of grasping actions (Rizzolatti, Fadiga, Matelli, et al., 1996). The time course of such activation has been examined using MEG, demonstrating inferior frontal cortex activation (homologous to the monkey premotor region) early on in the action representation for execution, imitation, and observation of action (Nishitani & Hari, 2000).
Sensorimotor training paradigms are useful for studying the acquisition of human mirror neuron system mapping. Evidence suggests that the system can adapt, and change with sensorimotor training so that new associations between goals and actions can be acquired (Catmur, Walsh, & Heyes, 2007). Importantly, experience can modulate the system, as shown in humans by corticoexcitability studies that involved counter-mirror movement training and resulted in existing mapping being ‘overridden’ when the normal movement was observed (Catmur et al., 2008, 2007). These types of studies present only the sensory component during the test phase of the experiment, and measure the action representation before and after training to elucidate modulations in the action-effect coupling.

The activity of the sensorimotor system has also been studied using MEG and EEG to investigate temporal dynamics and changes in synchronisation of populations of neurons. In particular, research has suggested that the sensorimotor action-observation response is indexed by the mu rhythm (Hari et al., 1998; Muthukumaraswamy et al., 2004; Neuper, Wörtz, Pfurtscheller, Christa, & Wolfgang, 2006; Pineda, 2005, 2008). Mu rhythm desynchronisation is described as a reduction in power for frequencies within ~8-12 Hz, recorded over sensorimotor cortex when an action is being performed (Pineda, 2005). Interestingly, this mu rhythm desynchronisation also occurs when participants passively observe an action. While the sensorimotor cortex is not a site where classical mirror neurons are found, it is still considered part of the network. Therefore, mu may still index mirror neuron activity by detecting modulation of the system, albeit further downstream from the actual mirror neurons (Pineda, 2005). Muthukumaraswamy and colleagues have demonstrated the human sensorimotor mu rhythm attenuation effect in a series of object-directed action studies (Muthukumaraswamy et al., 2004; Muthukumaraswamy & Johnson, 2004a; Muthukumaraswamy & Singh, 2008). Their findings suggest that there is some degree of specificity in the system, as observation of goal-directed movements such as gripping an
object, produced more mu desynchronisation than observing a hand merely forming a grip (Muthukumaraswamy et al., 2004).

So far the studies introduced have been object observation studies. However, action representation is not restricted to the visual (observation) domain and can also involve the auditory domain. In the monkey premotor cortex, neurons discharged when actions such as peanut cracking or paper ripping were heard and/or observed (Keysers et al., 2003; Kohler et al., 2002). A series of tests revealed varied properties of a large sample of neurons within the premotor cortex, whereby neuronal discharge was greater when the action was both seen and heard, compared to either seen or heard. These researchers suggest that particular neurons may contribute to an abstract representation of action, by coding the action independent of modality (Keysers et al., 2003). Additionally, some neurons discharged more for certain actions compared to others, such as peanut cracking compared to paper ripping (Kohler et al., 2002). This demonstrates that these neurons have differing degrees of specificity that may be modulated by experience, which is consistent with the aforementioned object observation studies of human action representation (Catmur et al., 2008; Muthukumaraswamy et al., 2004).

Action-perception coupling can be explored indirectly in humans, using musical stimuli as action-related sounds. Learning a musical instrument leads to action-effect coupling – musical performance (action) and perception (effect) become linked. One of the first studies that set out to explore action-perception coupling in musicians used MEG to compare pianists with non-pianists (Haueisen & Knösche, 2001). They found that pianists had an increase in contralateral motor cortex activity compared to non-pianists when listening to known piano pieces, demonstrating the action representation acquired by musicians during piano training.
A series of experiments using a different approach was carried out to investigate involuntary motor coactivation, with musicians playing music from a musical score (Drost et al., 2005a, 2005b). The pianists in these studies made more errors and responded more slowly when reading music if chords or intervals heard concurrently did not match the musical score. This suggests that movement induction by auditory stimuli in pianists interfered with ongoing playing. If the sound matched the visually specified interval or chord, there was a converse effect of facilitation of response (Drost et al., 2005a). Non-musicians tested on the same tasks did not show these effects, as they had not learned the action-effect associations.

The brain regions involved in the action-perception coupling effect were investigated further using fMRI in a number of studies. These include a study that investigated the auditory representation when pianists observed piano playing, rather than the more commonly investigated action representation of a visual stimulus intended to coactivate motor regions (Haslinger et al., 2005). They found fronto-parieto-temporal activation, further establishing the hypothesis that musicians develop action-perception coupling through musical training. Bangert and colleagues (2006) sought to reveal regions active during similar silent action observation, as well as action representation during passive listening to music in the same musicians. They focussed on elucidating the brain regions that were activated in both types of tasks and similarly reported activation in the abovementioned regions, suggesting the importance of these areas for sensorimotor integration. The audiomotor network was similarly revealed by another group, who also compared regions concurrently activated during motor and auditory tasks between pianists and non-pianists (Baumann et al., 2007). Taken together, it is clear that musical training leads to audiomotor coupling that enables action or auditory representation to occur when a musical stimulus is respectively heard or played.
Action representation during music notation reading has also been studied using mu rhythm desynchronisation in the EEG as an index (Behmer Jr. & Jantzen, 2011). In this study, mu desynchronisation occurred when musicians observed both music notation and performances, suggesting that these specific images are understood by this expert group and can be used to demonstrate the effect of sensorimotor integration. Importantly, their study extends the original idea of action representations (monkeys and humans observing another agent making the action), by showing that one does not have to be directly observing the action of others. Observing abstract associations (i.e. musical notation) can also result in an action representation effect. While Behmer Jr. and Jantzen (2011) specifically focussed on the visuomotor aspects of the action-effect coupling, the current study of this thesis investigates whether mu rhythm attenuates during music listening in absence of reading a musical score. If so, this would provide further support for the hypothesis that mu desynchronisation can index sensorimotor coupling.

In this initial investigation of action-listening mu rhythm effects, a group of pianists were recruited as participants. Here, the aim is to isolate the auditory aspect of the sensorimotor coupling, that has been investigated in fMRI studies, in order to determine if the mu rhythm may be used as an index for activity in the audiomotor network. According to previous literature described above, this highly skilled group already possesses action representation during passive listening of music. Therefore, it is predicted that pianists will show a significant attenuation of mu rhythm when passively listening to piano melodies.

### 2.2 Materials and Method

#### 2.2.1 Participants

Twenty right-handed (Oldfield, 1971) pianists participated in the experiment. All pianists had normal auditory acuity assessed by an audiometer (hearing thresholds for 250-
8000 Hz ≤ 25 dB HL, Amplitude T-Series, Otovation, LLC, USA). Data from three participants were excluded due to electromyography (EMG) activity indicating movement in over 50% of passive trials, and one additional participant was excluded due to a technical failure. The mean age of the remaining sixteen (13 female) pianists was 21.7 ± 3.91 years. Piano training commenced at a mean age of 6.4 ± 2.20 years, and mean number of years of playing was 14.8 ± 5.11 years. All participants gave informed consent and the experimental procedures were approved by The University of Auckland Human Participants Ethics Committee.

2.2.2 Procedure

The task was programmed using E-Prime software (http://www.pstnet.com). Pianists were instructed to listen to short extracts (7 s) of piano melodies. Figure 2.1 depicts the sequence of trial events. A behavioural task was inserted after each piano melody presentation, to ensure that participants kept attending to the piano melodies throughout the course of this passive (and not challenging) task – as was included in an fMRI study on action representation (Lahav et al., 2007). The behavioural task consisted of a short sequence of piano notes, randomly selected from a set of short sequences taken from each of the piano melodies. Participants were asked to indicate by button press whether they had heard the sequence in the longer piano melody directly before or not. This section of the trial was not intended for EEG analysis.
Figure 2.1 Passive listening task trial. A fixation cross was displayed on screen, participants listened to a piano melody, then to ensure attention to the stimuli was kept throughout the experiment, a brief extract of a piano melody was played, and they were asked to respond with whether the extract appeared in the melody or not.

Eight melodies were played in a random order and repeated to give 72 trials, presented in three blocks (Appendix 1). Participants had experienced playing all melodies. Stimuli were created in Sibelius 5 (Sibelius Software, London, UK, http://www.sibelius.com).

Participants were also asked to perform finger tapping movements on a computer keyboard, a task that has been used previously to determine the mu rhythm frequency band and confirm topography of mu desynchronisation over the sensorimotor cortex (Behmer Jr. & Jantzen, 2011). Participants tapped for 5 s, alternating between left and right hands, with a 5 – 5.5 s break in between each tapping period. Instructions were given in the form of two central red fixation crosses, with the right cross turning green to indicate right hand tapping, and left cross turning green to indicate left hand tapping.
2.2.3 Electrophysiological recordings

EEG was recorded from the scalp using 128-channel EGI amplifiers and Ag/AgCl nets (Electrical Geodesics Inc., Eugene, OR, USA). Recording sessions were carried out in an electrically shielded room. During the recording sessions, participants heard the melodies via etymotic earpieces (ER-2; Etymotic Research Inc., Illinois, USA). Continuous EEG was sampled at 1000 Hz, with 0.1 – 100 Hz analogue bandpass filter. Electrical impedances were maintained at an acceptable level for the high-impedance amplifiers of the EGI system (<40 kΩ) and data was recorded with Cz as a common reference. EMG recordings were monitored from the extensor digitorum communis (EDC) and flexor digitorum superficialis (FDS) of the right arm using disposable electrodes (Biovision, Wehrheim, Germany) at a sampling rate of 1 KHz with a 10-500 Hz Bessel bandpass filter. Any passive listening trials with detected movement were discarded before analysis. Although EMG was only recorded from two arm muscles, experimenters were able to view participants via a video monitor and did not observe any overt movement. Despite these measures, it is acknowledged that there may have been small activation of other muscles even if participants themselves reported that they understood the instructions and did not move during the trials.

2.2.4 Data preprocessing and analysis

Trials with EMG activity were discarded (mean rejection rate = 9.5% for audio, 17.1% for rest trials). EEG Data was re-referenced offline to the average reference bandpass filtered between 2 and 30 Hz and linear detrending was implemented. EEG recordings were segmented around the beginning of stimulus presentation, from -1000 to 5000 ms. In-house software was used to conduct time-frequency analysis of the data. Segmented EEG was convolved with a family of Gaussian tapered Morlet wavelets constructed at equally spaced frequency intervals of 1 Hz, that had a constant ratio of $f_0/\sigma t = 7$ (see Muthukumaraswamy & Johnson, 2004b).
The tapping task was analysed in order to confirm the topography of the mu rhythm and frequency band, displayed in Figure 2.2. EEG from the tapping task was segmented separately for right and left hand movement, and processed in the same manner as described above, then averaged across participants and across right and left hand conditions. Data was extracted from passive listening task trials for the mu frequency band (9 – 11 Hz), averaging across 1000 to 3000 ms after onset of the stimulus, to capture a central portion of the trial. A similar portion of the intertrial stimulus was extracted as rest. Further averaging was performed to collapse across two central electrode pairs for each hemisphere, which corresponded to the location of C3,CP3 and C4,CP4 in the 10-10 configurational system. These electrodes were selected to be consistent with previous literature (Behmer Jr. & Jantzen, 2011) and confirmed by the topography of mu desynchronisation (rest subtracted from tapping, 9 – 11 Hz) during the tapping task (Figure 2). For statistical analysis, a 2 x 2 repeated measures ANOVA was performed, with the within-subjects factors condition (audio, rest) and hemisphere (left, right).
Figure 2.2 Topographic plot of mu desynchronisation during left and right hand tapping (alternating index and middle finger), averaged over 1000 to 3000 ms after movement onset cue. Included in the figure are time-frequency plots for left (C3,CP3) and right sensorimotor cortices (C4,CP4), demonstrating the mu frequency band. Topographic plotting routine by S.D. Muthukumaraswamy, 2004.

2.3 Results

As illustrated in Figure 2.3, a main effect of condition (listening (audio) vs baseline (rest)) was revealed ($F(1,15) = 10.103, p = 0.006$). That is, passive listening to melodies resulted in significantly reduced mu rhythm power ($M = 0.096, SE = 0.043$) relative to rest ($M = 0.441, SE = 0.143$), demonstrating mu desynchronisation. There was neither a main
effect of hemisphere \((F(1,15) = 2.475, \ p = 0.137)\), nor a condition x hemisphere interaction \((F(1,15) = 0.015, \ p = 0.904)\).

2.4 Discussion

This initial investigation supports the hypothesis that musicians demonstrate action representation for music. Pianists demonstrated significant mu attenuation over sensorimotor areas during passive listening to piano melodies. Musicians have also demonstrated mu desynchronisation during sheet music reading and observing and listening to music performance (Behmer Jr. & Jantzen, 2011). Extending from this previous work that focussed on visual observation, the current study has shown that action representation can also be indexed by mu desynchronisation of EEG during purely auditory perception. Furthermore, together with object observation studies (Muthukumaraswamy et al., 2004;
Muthukumaraswamy & Johnson, 2004a, 2004b) and the musical notation observation study (Behmer Jr. & Jantzen, 2011), these results support the suggestion that the mu rhythm can indeed index mirror neuron activity, as outlined by Pineda’s (2005) review on action understanding.

Pianists in the current study revealed mu desynchronisation over both left and right sensorimotor cortices. This finding is consistent with other action representation tasks where participants observed hand movement or musical notation, although it has also been documented that the mu suppression may be lateralised to the left hemisphere for listening (auditory) tasks, in contrast with a bilateral effect apparent from observation (visual) tasks (Behmer Jr. & Jantzen, 2011; Hari, 2006; Muthukumaraswamy et al., 2004; Pineda et al., 2013). Furthermore, in the musical notation study (Behmer Jr. & Jantzen, 2011), the sheet music was observed by trumpet and violin players, who use both hands to produce sounds, and therefore mu attenuation in both hemispheres is not a surprising finding. In the current study, one might have expected a greater effect over left sensorimotor cortex as the melodies are heard in the mid-upper register so would specifically be played using the right hand. However, contrary to this expectation, the results of this experiment suggest that mu attenuation for musical sounds is a bilateral effect, regardless of how strongly a stimulus might be lateralised to one hand.

It is important to acknowledge that involvement of the vocal tract during passive listening cannot be eliminated, even though participants were asked to refrain from humming. Interestingly however, in an fMRI study, non-pianists did not demonstrate the action representation effect for listening that pianists did, despite both groups being able to accurately hum the melodies heard in their passive listening task (Baumann et al., 2007). This suggests that even if there was involuntary vocal tract activation, it likely does not confound the action representation effect found in the present study.
CHAPTER 2: ACTION REPRESENTATION IN PIANISTS

It has been argued that somatosensory feedback may play a role in the mu attenuation effect (Avikainen, Forss, & Hari, 2002; Rossi et al., 2002). During action observation studies, somatosensory regions may be activated due to a ‘mirroring’ type of response, which may be crucial in distinguishing another agent performing a movement as opposed to oneself (Avikainen et al., 2002). Other researchers suggest that since mu rhythm modulation is observed in differing brain regions from those reported in somatosensory feedback studies, it is unlikely that the desynchronisation is completely due to somatosensory feedback (Muthukumaraswamy et al., 2004; Pa & Hickok, 2008). The current study, as well as the musical notation observation study (Behmer Jr. & Jantzen, 2011) examined mu desynchronisation effects for more abstract learned associations, as opposed to observation of another agent making movements. Therefore, these studies differ in that they investigate how understanding of sensorimotor mappings modulates action representation, rather than examining somatosensory or mirroring processes. Moreover, somatosensory modulation may be an extension of the mirror neuron system (Pineda, 2008), and in this regard, could be an important aspect of the action representation response.

This experiment comprises of just one auditory task, and therefore has the limitation of a lack of comparison to other auditory tasks, which may have also revealed mu desynchronisation. Furthermore, only pianists were tested in this particular study and therefore conclusions that the effect is related to being musically-trained cannot be made with certainty. However, this is an initial investigation of the method of examining mu rhythm desynchronisation over sensorimotor cortex during musical listening, and the next chapter will address these issues by incorporating other auditory stimuli and testing non-musicians.

In summary, this experiment has shown that mu rhythm desynchronisation can be a potential index for audiomotor coactivation, supporting the idea that highly-skilled musicians demonstrate motor activity when passively listening to a well-learned music extract. This
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study provides the necessary foundation for further research on action representation and training-induced plasticity. These findings will be extended by investigating the modulation of action representation in non-musicians through musical training. If audiomotor coupling can occur after a brief training period and be indexed by EEG oscillatory measurements such as the mu rhythm, musical training studies could provide much-needed research toward the development of effective music-supported therapy for rehabilitating stroke patients. This will be the topic of the next chapter.
Chapter 3. The Effects of Musical Training on the Modulation of Mu Suppression

3.1 Introduction

It is well established that highly skilled musicians have acquired strong multimodal associations that result from musical training (see Herholz & Zatorre, 2012; Zatorre et al., 2007 for reviews). These learned associations have been useful for investigating sensorimotor integration and action representation for sounds. For example, involuntary motor activity occurred when pianists listened to music they had previously played, as demonstrated by MEG activation in primary motor cortex (M1) (Haueisen & Knösche, 2001). Similar action representation for rehearsed music was also revealed using TMS, as corticospinal excitability increased when pianists were listening to a rehearsed musical piece (D’Ausilio et al., 2006).

The converse direction of coactivation has also been studied, where observation of silent piano playing activated the auditory cortex in musicians (Haslinger et al., 2005). Coactivation in both directions was revealed using fMRI, where listening to a melody activated a fronto-temporal sensorimotor network, and silently playing a melody activated a similar network of regions in pianists (Bangert et al., 2006). Such studies have helped to establish that musical training creates and/or strengthens links between sensory and motor areas, to an extent that only one of the modalities is required to activate the sensorimotor network.

Importantly, musical training contexts have also provided evidence for short-term training-induced plasticity, and demonstrated that integration of sensory and motor perception-action processes after even a brief period of time may be crucial for successful training. One study compared unimodal and multimodal short-term training, and reported that when training involved hearing the auditory stimulus alone (i.e. did not incorporate playing), pitch and timing ability did not improve, and ERP responses were not modulated as much as
those who had undergone audiomotor training (Lappe et al., 2008). In addition, training-induced plasticity has been demonstrated by comparing slow-wave EEG before and after participants underwent audiomotor training to learn to play melodies (Bangert & Altenmüller, 2003). In this study training was multimodal (audiomotor) but EEG tasks were presented unimodally. Similarly to the previously mentioned fMRI study with pianists (Bangert et al., 2006), participants in this study also showed involuntary auditory coactivation during silent playing as well as involuntary motor coactivation during passive listening of melodies (after five weeks of training had been completed). These studies demonstrate that the tight sensorimotor coupling shown by musicians can also be acquired after short-term training.

In the visuomotor domain, studies have demonstrated that different types of observation-action tasks result in modification of the action representation to varying degrees. For example, goal-directed actions are associated with greater mu rhythm desynchronisation than non-goal-directed actions (Muthukumaraswamy et al., 2004). If action-listening is indeed similar to observation-action in the involvement of the mirror neuron system, as discussed in the previous chapter, the sensitivity of the mu suppression effect could be useful for gaining further insight into properties of audiomotor systems. Music perception requires complex processing of separate elements such as pitch and rhythm, and if the mu suppression effect is adequately sensitive, the differing effects that specific elements of the action-listening stimuli have on the audiomotor response may be elucidated.

Mu suppression has been examined in a musical notation observation-action paradigm – however this study compared already-proficient musicians and non-musicians, and did not incorporate a training period (Behmer Jr. & Jantzen, 2011). I extended these findings with the study reported in Chapter 2, by establishing that mu suppression can also be measured for (non-visual) action-listening tasks, however that study also had highly skilled musicians as participants. Here therefore, the aim is to extend these cross-sectional type of studies and
investigate modulation of mu suppression within individuals, who are trained over a short period of time to a sufficient level of proficiency on a musical task.

An advantage of using novel complex action-related sounds such as those learned on a musical instrument, is that training can be restricted to specific sound-action mappings. In other words, if motor coactivation is detected after training, one can determine if the action representation occurs only for the specific sounds that were learned during the sound-action mapping, and not for other sounds. One study that addressed this, demonstrated that involuntary motor coactivation (in fronto-parietal regions) was only found when participants passively listened to melodies that they had newly acquired actions for, and was not found for other melodies (Lahav et al., 2007). Participants in this study learned to play one musical piece over the course of five days. Interestingly, a left posterior premotor area of interest (the IFG) appeared to have a differing pattern to the right across the three listening tasks participants heard during an fMRI session after training. The right IFG appeared active across all presented melodies, whereas the left IFG was clearly active only when participants heard the trained melody compared to either untrained notes or a melody that was comprised of the same notes in a different order than the trained melody. Although these researchers did not highlight this as their main finding, this hemispheric difference could be seen as consistent with motor learning studies that suggest that during initial phases of learning, some regions of the network are activated to a greater extent relative to when proficiency is attained; i.e. some premotor areas are differentially recruited during different phases of learning. Indeed, in a review of motor acquisition studies, the right hemisphere was reported to be involved during early stages of learning, whereas a shift to the left hemisphere was revealed later in the time-course of learning – regardless of which hand was trained (Halsband & Lange, 2006).

While Lahav and colleagues (2007) stress the importance of having acquired specific sound-mappings in one’s motor repertoire, others argue that a rhythmic stimulus alone is
sufficient to produce these motor coactivation patterns during passive listening, as it is human nature to ‘move to’ a beat in music (Chen et al., 2009).

Humans move to music from an early age (Phillips-Silver & Trainor, 2005). Does this seemingly automatic response suggest that our sensorimotor networks already have the necessary integration required for action representation during listening to music? This viewpoint would suggest that we have an association of sound to movement, without having to acquire expertise in music performance, or understand what action is required to produce the heard sound. The sensorimotor system could be more generalised; i.e. hearing any musical or rhythmic stimulus will involve an involuntary motor response regardless of how proficient you are in playing a musical instrument, and specific sound-action mappings do not need to be understood.

Evidence for the role of audiomotor networks in rhythmic listening comes from fMRI studies that investigated synchronisation processes (i.e. tapping to the beat) (Chen et al., 2009). For example, it was shown that activity in audiomotor regions could be modulated by rhythm complexity when non-musicians tapped to rhythms (Chen, Penhune, & Zatorre, 2007). In this study, activation was not examined when participants listened to the rhythm to prepare for synchronisation, as the authors note that in such tasks, where one listens to rhythms before having to synchronise, or tap, to the beat the premotor network may have been activated because subjects were preparing to make the movements. This issue was addressed in a further study by Chen and colleagues (2008), where they sought to differentiate between rhythm perception for reproducibility and rhythm perception without the anticipation of having to reproduce the rhythm. Both types of listening tasks activated a network of premotor regions indicative of action representation, but listening with anticipation resulted in an additional region of activation in ventral PMC. This suggests that
action representation can occur at varying degrees, and the differential effects for different tasks can be detected using brain imaging methods.

Audiomotor networks were also activated during a same/different rhythm perception task (Grahn & Brett, 2007). A distributed network including SMA, dorsal premotor cortex, basal ganglia, ventral PFC, STG, cerebellum and insula was found to be active, although M1 was not, which the authors suggested confirmed that subjects did as asked and did not move during the passive listening task. A comparison was also made between musicians and non-musicians. Musicians showed greater activation compared to non-musicians in SMA, right PMC and bilateral cerebellum, despite both groups attaining similar accuracy for the discrimination task. Nevertheless, both groups showed activation in regions incorporated in a network that the aforementioned sensorimotor studies describe as activated during passive listening.

Similarly, Grahn and Rowe (2009) also reported activation of a distributed network of sensorimotor regions during purely perceptual rhythm tasks, although the coupling of striatal regions to these cortical sensorimotor regions was emphasised in this investigation. Again, this action representation response was revealed in both musicians and non-musicians. Interestingly, non-musicians showed similar coupling patterns for the different types of beats that were presented in the study, whereas musicians demonstrated a different modulation of response depending on beat properties (greater coupling for beats defined by volume contrasts than duration changes).

These studies suggest that the specific nature of the task may indeed affect the coactivation of motor regions. Furthermore, irrespective of musical training experience and listening task differences, the rhythmic element of music may activate the sensorimotor network. One index for sensorimotor response to rhythms, may be mu suppression (Pineda,
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2005). Mu suppression may occur while one listens to rhythmic stimuli without having undergone musical training. Even if the experience of mapping sounds to specific actions is not required for action representation to occur when rhythms are heard, audiomotor training could still strengthen sensorimotor integration for rhythmic perception so that post-training effects still occur. Support for this view comes from a recent study that showed multimodal training sessions enhance musical expectations for learned rhythmic patterns (Lappe, Trainor, Herholz, & Pantev, 2011). One group of participants learned to play a melody in eight training sessions. These participants were referred to as the multimodal training group. A second group, referred to as a unimodal training group, were asked to judge the accuracy of the performance of the multimodal training group’s performance. Critically, the multimodal training group demonstrated enhanced MMN responses to rhythmic deviation after training while the unimodal evaluation group did not show modulation of the MMN. These findings corroborate the findings mentioned previously (Lappe et al., 2008) that demonstrate the importance of the integration of sensory with motor processes for action representation effects.

To further investigate the specificity effects of audiomotor training, I recruit participants who had not experienced musical training in order to examine short-term training effects on audiomotor coactivation, which may relate to human mirror neuron systems. Participants learn specific sound-action mappings through an adaptive training paradigm and the change in sensorimotor response to hearing sounds related to those encountered in training will be investigated by measuring mu suppression.

EEG will be recorded in a session prior to training and a second session after participants reach a performance criterion. This study seeks to determine if mu rhythm over sensorimotor cortex during listening to musical sequences attenuates after short-term musical training. I also aim to address three additional questions: 1) does greater mu suppression occur for the
specific sounds that are mapped during training, as opposed to sounds that are related but not mapped during training?; 2) do non-musicians show mu suppression when listening to a rhythmic sequence and does training affect this response?; and 3) if mu suppression does occur, are there any differences between the left and right sensorimotor cortex?

3.2 Materials and Method

3.2.1 Participants

Participants were right-handed, as assessed by the Edinburgh Inventory (Oldfield, 1971), and had no more than one year of formal musical training. All participants had normal auditory acuity as assessed by an audiometer (hearing thresholds for standard range 250-8000 Hz ≤ 25 dB HL, Amplitude T-Series, Otovation, LLC, USA). Twenty participants commenced the training, but seven did not reach the performance criterion, and therefore did not complete the entire experiment. Therefore, data from 13 participants (eight male, 5 female; age 24.3 ± 5.74 years) were included in the analysis. All participants gave informed consent and the experimental procedures were approved by The University of Auckland Human Participants Ethics Committee.

3.2.2 Adaptive training paradigm

The aim of the training aspect of the experiment was for participants to acquire auditory-motor mappings for piano tones. Participants were trained using interactive training software (see Bangert & Altenmüller, 2003 for further details). Three second long tone sequences consisting of notes between C5 – G5 were generated online using values for the parameters (a) number of notes; b) range of notes; c) note length range) that met the criteria for a particular level (smaller values for lower levels). These tone sequences were played to the participant, who was then to attempt to reproduce the sequence on a keyboard. Each session began at Level 1 (easiest) and participants had to progress beyond Level 6 to complete the
training part of the experiment. The sequence of events for a trial is depicted in Figure 3.1. Each trial started with the presentation of the sequence of notes, then a white keyboard icon appeared to indicate that participants must attempt to play what they have just heard. This icon turned red when 3000 ms passed, indicating to participants to stop playing, and then the wait screen appeared. Participants started each training trial when they were ready.

Figure 3.1 Trial sequence of the training. Participants listened to a tone sequence, attempted to play it back, and pressed the pedal to begin the next trial when ready. Sequences of notes were randomly generated online.

The software is adaptive; trials increased or decreased in difficulty according to the participant’s accuracy in three aspects of performance: pitch, timing and dynamics. Table 1 presents training level parameters. Weighting criteria for accuracy were: Pitch errors (wrong
key pressed), Timing errors (key pressed outside 1/16\textsuperscript{th} of the beat), dynamic errors (MIDI velocity differed from loudness more than 10%).

Table 1.

*Training levels and corresponding parameters. Range of Notes and Note Types were presented in random sequences.*

<table>
<thead>
<tr>
<th>Level</th>
<th>Range of Notes</th>
<th>Number of Notes</th>
<th>Tempo (bpm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>C – D</td>
<td>♩ ♩ ♩</td>
<td>60</td>
</tr>
<tr>
<td>2</td>
<td>C – D – E</td>
<td>♩ ♩ ♩</td>
<td>60</td>
</tr>
<tr>
<td>3</td>
<td>C – D – E – F</td>
<td>♩ ♩ ♩</td>
<td>60</td>
</tr>
<tr>
<td>4</td>
<td>C – D – E – F – G</td>
<td>♩ ♩ ♩</td>
<td>60</td>
</tr>
<tr>
<td>5</td>
<td>C – D – E – F – G</td>
<td>♩ ♩ ♩ ♩ ♩</td>
<td>80</td>
</tr>
<tr>
<td>6</td>
<td>C – D – E – F – G</td>
<td>♩ ♩ ♩ ♩ ♩ ♩ and ♩</td>
<td>80</td>
</tr>
<tr>
<td>7</td>
<td>C – D – E – F – G</td>
<td>♩ ♩ ♩ ♩ ♩ ♩ ♩ and ♩</td>
<td>80</td>
</tr>
<tr>
<td>8</td>
<td>C – D – E – F – G</td>
<td>♩ ♩ ♩ ♩ ♩ ♩ ♩ ♩ and ♩</td>
<td>100</td>
</tr>
<tr>
<td>9</td>
<td>C – D – E – F – G</td>
<td>♩ ♩ ♩ ♩ ♩ ♩ ♩ ♩ ♩ and ♩</td>
<td>100</td>
</tr>
<tr>
<td>10</td>
<td>C – D – E – F – G</td>
<td>♩ ♩ ♩ ♩ ♩ ♩ ♩ ♩ ♩ ♩ and ♩</td>
<td>100</td>
</tr>
</tbody>
</table>

The levels progressed (increased, decreased, or stayed the same) depending on performance of previous trials. Each session was terminated when the participant’s performance curve was at exponential saturation (i.e. when they reached their maximal level and ceased moving up or down levels). Participants heard the usual sound feedback of the piano, but there was no explicit feedback as to the accuracy of their reproduction (although participants could infer how their performance was going if the next trial increased or decreased). There were no visual or verbal cues such as tone names, music notation, and after their right hand was placed over the correct group of keys, participants had their hands shielded from view during the trials (see Figure 3.2).
Figure 3.2 Training setup: Participants had their hand placed on the correct group of keys, and during training their hand was shielded – no visual feedback. Participants focussed on the screen which displayed instructions as the training proceeded. A foot pedal was used for proceeding to the next trial.

3.2.3 EEG procedure

EEG was recorded during two sessions in an electrically shielded, sound-attenuated room. The first session preceded training and participants returned for the second session after they had completed the training to the level required. The EEG sessions consisted of Rest, Audio, and Audiomotor blocks. The Audio block consisted of three conditions, randomised in presentation – (a) Audio-T: tone sequences generated using the same notes as heard in the training paradigm (C5-G5), (b) Audio-U: tone sequences generated using notes of lower pitch (C3-G3), (c) Audio-W: rhythmic sequences (woodblock) (Figure 3.3). Therefore, there were a total of five conditions.

Figure 3.3 Examples of trials: a) Audio-T; b) Audio-U; c) Audio-W.
Trials proceeded as depicted in Figure 3.4. In Audio trials, participants were instructed to listen to these 3000 ms sequences and asked to keep still and relaxed. After an inter-stimulus interval of 6000 ms the next tone sequence was played. The stimuli were synthesized online by the same software as in the training procedure, and were presented at a constant level of difficulty (Level 6 from the training paradigm). As in the training sessions, participants kept fixated on the centre of the computer monitor, where the instructions at each point of the trial were given. During the Rest block, participants were instructed to sit still with arm relaxed, fixating on the centre of the screen (Figure 3.4a).

In the Audiomotor block, participants were asked to listen to a tone sequence (generated using the same notes as in the training paradigm, at Level 6) and were asked to playback the sequence (as in the training paradigm). Playback duration was constrained to 3000 ms with computer instructions. After a 6000 ms interval, the next trial began (Figure 3.4b). Blocks were presented in a counterbalanced manner across participants, and in total there were 40

![Figure 3.4 a) Audio and Rest trials. b) Audiomotor trials.](image)
trials per condition. Stimuli were presented binaurally using etymotic earpieces (ER2; Etymotic Research Inc., Illinois, USA).

3.2.4 Electrophysiological recordings

EEG was recorded from the scalp using 128-channel Electrical Geodesics amplifiers and Ag/AgCl nets (Electrical Geodesics Inc., Eugene, OR, USA). Continuous EEG was sampled at 1000 Hz, with 0.1 – 100 Hz analogue bandpass filter. Electrode impedances were maintained at an acceptable level for this EGI system (<45 kΩ) and data was recorded with Cz as a reference.

EMG recordings were monitored from the EDC and FDS of the right arm using disposable electrodes (Biovision, Wehrheim, Germany) at a sampling rate of 1 KHz with a 10-500 Hz Bessel bandpass filter. Any passive listening trials with detected movement were discarded before analysis. In addition to the EMG monitoring, experimenters were able to view participants via a video monitor and did not observe any overt movement. Finally, participants self-reported understanding the instructions and that they did not move during trials. Despite these measures, we acknowledge that there could have been small activation of other muscles that we did not monitor.

3.2.5 Data preprocessing and analysis

EEG data was re-referenced offline to the average reference (thus creating 129 electrodes) (Betrand, Perrin, & Pernier, 1985). Any trial where EMG activity was detected by visual analysis was discarded (mean rejection rate 6%, range 0 - 40%). The data was time-locked to a trigger pulse that occurred at the onset of the first note of the stimulus and the stimulus sequence was then sub-divided into five non-overlapping epochs of 512 samples per trial, giving a maximum of 200 epochs per condition. Fast Fourier transforms (FFTs) were computed for spectral power analysis and the mean power was calculated for the mu band.
Data was then subjected to a logarithmic (log) transformation in order to stabilise variances (Gerloff et al., 1998).

Individual mu rhythm bandwidths were defined by a procedure based on an action-observation study (Muthukumaraswamy et al., 2004). In brief, the Audiomotor condition was subtracted from the Rest condition and this spectral subtraction was plotted topographically for each participant. The 2-Hz wide frequency band with a topography plot that best resembled mu desynchronization as found in previous studies (McFarland et al., 2000; Pfurtscheller, Neuper, Andrew, & Edlinger, 1997) was selected. Figure 3.5 displays the topography of mu desynchronisation averaged across all subjects, and indicates the cluster of electrodes used in the analysis.

Figure 3.5 Topographic map of mu desynchronisation during piano playing (Audiomotor-Rest, 9.8-11.7 Hz). Pre-training (a) topography was similar to that measured post-training (b). Cluster of the 8 electrodes each around C3 and C4 are displayed.

The Rest condition was then subtracted from the three Audio block conditions in their defined 2 Hz wide band. The cluster of eight electrodes around the standard C3 (left) and C4 (right) positions used for statistical analysis was based on the previous action-observation
study (Muthukumaraswamy et al., 2004). The electrodes are depicted more clearly in Figure 3.6.

A three-way repeated measures ANOVA was conducted with within-subjects factors of Session (Pre/Post), Hemisphere (left/right) and Condition (Audio-T/Audio-U/Audio-W). Pairwise comparisons were investigated for any significant effects and adjusted using Bonferroni correction. As the Audiomotor-Rest subtraction was used to define each participant’s mu frequency band, this condition was not included in the statistical analysis.

3.3 Results

3.3.1 Training performance

Thirteen participants reached the required proficiency (Level 6). It was intended that training sessions would occur 2-3 times a week for 5-8 weeks, so that each participant had 15 training sessions. Duration of training session varied from ~10 – 22 minutes. However, only three participants had reached Level 6 proficiency by the 15th session. It was decided that
participants that were willing could continue with training, in order to reach the sufficient level to be able to carry out the audiomotor task in the post-training EEG session. The number of sessions that participants took ranged from 15 to 56 sessions and mean accuracy in the post-training audiomotor task was 67%.

3.3.2 Task-related power analysis

The repeated measures ANOVA with Session (Pre, Post), Hemisphere (Left, Right) and Condition (Audio-T, Audio-U, Audio-W) as factors revealed neither main effects nor interactions (all $p > 0.05$). (Main effect of Session $F(1,12) = 0.004, p = 0.948$; Hemisphere $F(1,12) = 0.051, p = 0.825$; Condition $F(1.1,13.1) = 0.016, p = 0.676$; and Interaction between Session and Condition $F(1.1,13.4) = 0.277, p = 0.633$; Session and Hemisphere $F(1,12) = 2.281, p = 0.157$; Hemisphere and Condition $F(1,24) = 2.229, p = 0.129$.) Figure 3.7 displays the mean log mu task-related power (i.e. mu suppression) for each condition.
Due to the lack of significant effects from the main analysis, a subsequent analysis was performed. Because the EEG sessions included a task that required participants to play notes on the piano, the pre-training mu desynchronisation was examined to explore possible effects if the mere act of pressing piano keys to produce sounds was sufficient to modulate mu rhythm. Mu suppression in the three Audio (Trained, Untrained, Rhythm-woodblock) conditions pre-training were not different to the baseline rest condition (all $p > 0.05$).
3.4 Discussion

Contrary to previous research that formed the basis of this study, mu suppression modulation was not found post-training in non-musicians who underwent an adaptive training regime for several weeks. The current findings of EEG mu desynchronisation measures over sensorimotor cortex may appear to contradict the results of previous fMRI studies that showed action representation effects specifically for trained musical sounds (Bangert et al., 2006; Lahav et al., 2007), as well as studies that showed rhythm-induced action representation regardless of musical training experience (Chen et al., 2008; Grahn & Brett, 2007). Due to the lack of post-training effects I was unable to elucidate whether there was a difference between mu suppression modulation for specific sounds or rhythms. Hemispheric effects were also unable to be investigated.

One possible explanation for the apparent disparity with previous literature is that, although all participants included in the analysis completed training to a sufficient level, unexpectedly, many participants struggled with the training phase. This was a surprising finding, having based the training protocol on an adaptive training software developed by Bangert and Altenmüller (2003). Participants in that study had fewer sessions to achieve the required skill level. In that study, all the non-musicians trained for ten 20 minute sessions (five weeks of training) and all achieved proficiency up to the required level without issue (M. Bangert, personal communication, September 10, 2008). Similarly, the non-musicians in another training study became proficient in playing the piano piece they were to learn (Lahav et al., 2007), although learning one brief musical piece with a pre-recorded backing band (guitar, bass, drums) accompaniment during training could arguably be more motivating than the type of adaptive training paradigm used in the current study.
Instead of having participants learn a single melody during training as Lahav and colleagues (2007) used, I aimed to have participants link specific sounds (each piano note) to specific actions (each finger) rather than a specific audiomotor sequence. This was in order to examine action representation for abstract sound-action mappings, instead of investigating sequence memory processing. Perhaps sequence processing is an important part of sensorimotor coupling that occurs from training. As well as general motivation for learning a complete musical piece, as opposed to the challenge of playing different sequences of notes, perhaps the training aspect of this study would have been more successful if the training paradigm implemented had incorporated both elements. In a recent study, participants learned a melody first, and then reinforced audiomotor associations that were specific mappings by presenting random melodies that they then had to play back (Chen, Rae, & Watkins, 2012). The planning of known motor sequences did not occur in the random melody phase of learning as the order of the pitches changed each trial, but the initial melody learning could have aided the latter training. This study examined brain activation both for learned melodies and random sequences, and found the ventral PMC additionally affected during melody listening. In our design, this first step of the training regime might have provided a better grounding for learning the specific sound-action mappings. Nevertheless, the non-musician group from the original adaptive training study did persevere and succeeded in the training within the set number of sessions (Bangert & Altenmüller, 2003).

This brings us to the following speculation, albeit presented with caution as it involves an interpretation of a null finding. The stimuli in the current study are generated randomly. This presents a major difference, as highlighted above, to stimuli used in the study of Lahav and colleagues (2007). In their study, stimuli presented during the fMRI session were the exact audiomotor sequences that were learned during the training sessions. These were the only type of stimuli that showed modulation of activation levels in the left IFG. Perhaps it is
the action representation for learned audiomotor sequences revealed here, which would not have shown in the current study as stimuli were randomised sequences, and not necessarily the same as the audiomotor sequences encountered in the training sessions. In addition, the length this group took to train to performance criterion, in comparison to the short training time to learn a musical piece (5 days), suggests that people learn audiomotor sequences with more success than specific sound to action mappings. One could further speculate that sequences or melodies may be more similar to goal-directed action, whereas a specific sound-action mapping is not as goal-directed. If this is the case, in accordance to object observation-action research, more mu desynchronisation might be expected for melodies (Muthukumaraswamy et al., 2004). However, again it must be noted that the adaptive training paradigm in the current study was modelled on that used in a previous study, and the participants in that study were presented the same randomised sequences in training, and still learned the specific sound to action associations within a shorter time period (Bangert & Altenmüller, 2003).

Bangert and Altenmüller (2003) also trained a ‘no-map’ group who did not acquire specific sound-action mappings as the piano notes were randomly designated each trial. However, they improved in timing and dynamic accuracy after eleven training sessions, and it would have been interesting to test modulations in action representation if they had been presented with an auditory woodblock sequence in the EEG sessions.

However, in making these speculations, it is acknowledged that caution must be taken when accepting the null hypothesis. Even though the results of this study appear to go against those of previous related studies, given that the combination of mu suppression measurement and action representation response in an audiomotor training study has not been investigated before, it is possible that such an association cannot be detected by examining mu suppression effects after this type of training procedure. Furthermore, the Audio-T and
Audio-U conditions in the current experiment shared the same notes (C, D, E, F, G), even though they were in an entirely different range of the piano. Incorporating an additional set of stimuli that differed in this parameter (e.g. notes in a different key, or modality) may have differentiated between these piano tone conditions.

With regard to the training difficulties that arose, it is likely that having visual cues in the training would have helped participants gain accuracy and train more proficiently. However, as with both of the seminal audiomotor studies (Bangert & Altenmüller, 2003; Lahav et al., 2007), the aim was to focus on audiomotor integration in this study, and I deliberately excluded any visual cues in the training process. According to Lahav and colleagues (2007), the focus on audiomotor coupling could be enhanced if involvement of a visuomotor component in training was reduced. This view was also taken by Chen and colleagues (2012), who asked participants to close their eyes to eliminate visual input.

It appears that the extended period of training required by the current study’s participants to reach the performance criterion (and 7 did not reach criterion and therefore did not complete the experiment) may indicate that this particular group of people were not rapidly learning individual sound-action mappings, in contrast to the participants in Bangert and Altenmüller’s (2003) study who had faster learning rates. This points to a group difference between the non-musicians in this study compared to Bangert and Altenmüller’s (2003), which may contribute an explanation as to why we did not find a significant pre-post difference as they did. Perhaps the small number of participants in this study (N = 13) also contributed to the discrepancy in results; however, groups of 9 (‘map’ group) and 8 (‘no-map’ group) non-musicians participated in the previous study (Bangert & Altenmüller, 2003).

The other aforementioned studies also appeared to have faster learners – although as discussed, the Lahav and colleagues (2007) used audiomotor sequences rather than
randomised sequences. Moreover, participants in the experiment by Chen and colleagues (2012) trained for only 20 minutes, suggesting again that the current study’s participants consisted of slower learners, although additional reasons for the contrast in training times required are given above. An interesting comparison to make between their study and this study is the note types used for their experiment. Their melodies and random sequences consisted of 5 crotchets (i.e. 5 notes of even duration), whereas here the performance criterion was set at Level 6 of the training paradigm, which included a quaver note. Having to incorporate this additional rhythmic element into achieving accurate playback might have contributed to the difficulty the participants had to reach performance criterion, and led to longer training times. Again however, this does not explain how Bangert and Altenmüller’s (2003) participants successfully reached their performance criterion (same number and types of notes as ours but even faster tempo!). Here again, training results point to a difference between participant groups.

In order to explore individual differences, the effect of training duration required to reach performance criterion was informally examined. Training duration and mu suppression difference between pre- and post-training were plotted for Audio-T, Audio-U and Audio-W. No obvious relationship was observed in the scatterplots, as expected, given that the acquisition of sound-action mappings was important, rather than exposure to stimuli. Chen and colleagues (2012) also examined individual differences in their fMRI study, and they found a negative correlation between performance accuracy and percentage BOLD signal change. We explored the comparative relationship in the current study but found no pattern when participants’ performance was plotted again mu suppression.

Our hypotheses were based on the culmination of findings from audiomotor, rhythm and mu suppression studies (Bangert & Altenmüller, 2003; Chen et al., 2009; Grahn & Brett, 2007; Lahav et al., 2007; Muthukumaraswamy et al., 2004). Our study did not parallel the previous
findings. However, another possibility for a lack of mu suppression in any of the post-training tasks could be that non-musicians acquire audiomotor coupling very quickly, as they play notes on the piano during the AudioMotor block in the pre-training EEG session. Even though they had not acquired specific sound-action mappings, the act of playing the piano notes could well have made sufficient associations between finger movements making piano sounds to strengthen audiomotor connections in the one EEG session. We also explored this informally, by performing an ANOVA on the pre-training session data separately. The three Audio (Trained, Untrained, Rhythm-woodblock) conditions pre-training were not different to the baseline rest condition. Therefore, the expected pattern of results for pre-training tasks was found and an initial change in audiomotor coupling during the pre-training EEG session cannot explain why our results are in contrast to those previous musical training studies which revealed action representation in participants post-training.

Overall, these results may suggest that either the adaptive training paradigm did not sufficiently strengthen audiomotor coupling for mu suppression to occur, or the mu rhythm suppression technique I selected to utilize is not as sensitive as other measures, such as slow wave EEG, to detect post-training action representation effects in tasks that presented the sensory component learned in training.

Nevertheless, the present study highlights the need for training methods to be investigated, and individual preferences for training techniques to be examined. Individual differences have recently been explored by Engel and colleagues (2014), who showed that training ability may be influenced by the integrity of white matter tracts. Fractional anisotropy, commonly used as a measure of white matter integrity, of the corticospinal tract and superior longitudinal fasciculus (SLF) was shown to correlate with speed of learning. These tracts included connections between sensorimotor regions, and the authors suggest that their results demonstrate that the corticospinal and SLF tracts are involved in audiomotor
learning, as individual differences in these tracts relate to the differences in learning ability for a musical task (Engel et al., 2014).

Perhaps comparing various training techniques and refining the EEG procedure, the mu rhythm may yet prove to be sensitive enough to detect action representation as it has been shown to be detected in musicians during passive listening. In addition to structural connectivity such as those investigated by Engel and colleagues (2014), it would also be of interest to determine if connectivity between regions modulates through training. The next study aims to investigate cortico-cortical coupling by using EEG measures of functional connectivity.
Chapter 4. The Effects of Musical Training on EEG Coherence

4.1 Introduction

Musical training leads to associations between certain sounds and specific actions. The development of these associations requires the strengthening of connections between auditory and motor regions of the brain (Zatorre et al., 2007). One method of investigating the formation of putative audiomotor associations is to compare regional coherence of oscillatory activity before and after training. Coherence, in this context, measures the linear dependency between two signals, and oscillatory signals from EEG have been used extensively to study cortico-cortical functional connectivity (Gerloff, 2002; Weiss & Mueller, 2003). High cooperation or functional coupling between brain regions is argued to be reflected in high coherence values between EEG signals recorded over those regions (Andrew & Pfurtscheller, 1996).

Studies of sensorimotor tasks have focussed on oscillatory activity in various frequency bands. For the study of sensorimotor coupling, particular emphasis is placed on alpha and beta band coherence (Andres & Gerloff, 1999). Most commonly, coherence measures for rest or baseline tasks are subtracted from coherence measured during the tasks of interest; this is termed task-related coherence (TRCoh). Increased coherence during a task relative to rest is taken as evidence for sensorimotor integration. An early study of TRCoh during finger movement tasks demonstrated that the functional connectivity in alpha (8-12 Hz) and beta (13-20Hz) frequency bands increased for more complex sequential motor tasks (Manganotti et al., 1998). Another study investigated similar frequency bands and found beta to be the frequency band with the greatest modulation depending on whether the task required visuomotor integration (Classen, Gerloff, et al., 1998). They reported an increase in coherence between central and occipital electrodes during visuomotor tracking tasks,
compared to either visual or motor only tasks, demonstrating the involvement of beta coherence modulation in integration. The mu rhythm, as discussed in earlier chapters, has been suggested as an index of sensorimotor integration and spans the alpha range (8-12 Hz) over sensorimotor cortex (Pineda, 2005). A more recent EEG study focussed on this particular frequency band for investigating changes in connectivity due to the acquisition of visuomotor and audiomotor tracking precision skills (Blum et al., 2007). They found inter- and intra-hemispheric learning related changes but only for the degree of phase locking and, in contrast to previous studies (Andres & Gerloff, 1999; Gerloff & Andres, 2002), not for coherence measures. Blum and colleagues (2007) acknowledge that phase locking and coherence are similar measures, and additionally report similar but not significant effects for coherence. They discuss that connectivity may vary depending on the type of task used, as unlike previous studies, the task they administered required continuous adaptation as tracking cues were continually changing. Despite discrepancies in tasks and modalities, these studies demonstrate the value of examining both alpha and beta coherence modulations for sensorimotor integration.

In addition to the appropriate selection of frequency bands, when investigating functional coupling during musical training, one must also consider which brain regions are involved in the integration processing. In fMRI studies, recruitment of a fronto-parieto-temporal network including motor, premotor, supplementary motor and secondary sensory areas have been shown to contribute to auditory and motor integration (Baumann et al., 2007; Chen et al., 2012; Haslinger et al., 2005). Different regions within the network may be involved in different processes. For instance, the ventral premotor area is a key region for action-observation matching processes, based on visuomotor studies on monkeys (Keysers et al., 2003; Kohler et al., 2002). The dorsal premotor cortex on the other hand, is argued to be
involved in complex sensorimotor integration, such as audiomotor associations learned during piano training (Zatorre et al., 2007).

Learning a musical task requires more than the skill to play a complex sequential movement. Integration between auditory and motor processes is also crucial. Thus, musical tasks may demonstrate different changes of coherence to the motor and sensorimotor studies mentioned above. Few studies on audiomotor integration use electrophysiological methods to investigate changes in functional connectivity after music training. Musical training effects on TRCoh have been studied in stroke patients, where a form of therapy is being developed that involves patients undergoing a training regime on either a piano keyboard or drum pad that produces piano sounds (Altenmüller et al., 2009). This study demonstrated increased functional coupling in the beta (18-22Hz) band but not alpha (8-12Hz) band after audiomotor integration was established by music-supported therapy (MST). Here, a broader exploratory approach incorporating coverage of the whole head was carried out to capture any post-therapy modulations (Altenmüller et al., 2009), whereas other studies of training-related plasticity have targeted specific sensorimotor areas that have been highlighted by previous literature, such as fronto-parietal networks (Blum et al., 2007).

Furthermore, in many of the aforementioned EEG coherence studies, participants perform the actual movements that they have learned during the training phase of the experiment. It would therefore, be interesting to determine if action representation in the absence of movement can also be investigated using coherence measures. Activation in motor regions during passive listening has previously been demonstrated in pianists using MEG (Haueisen & Knösche, 2001). This study found greater activation exclusively in the contralateral M1 in their pianist group compared to non-pianists (and even demonstrated a significant difference between listening to notes played by the thumb compared to the little finger in M1), with no activation differences in typically implicated regions such as the SMA,
premotor cortex and parietal regions. They suggested that this may be because there is no need for highly-skilled participants to recruit these supplementary regions. In addition, the comparison group were singers, who had experience in performing music, and thus may also have similarly developed action representation in supplementary motor areas. This would then result in the specifically localised M1 differences that were shown, as singers would not have the action representation effects in the hand region of M1 that pianists showed.

Non-musicians have also been studied after undergoing piano training, in order to investigate if changes in slow wave EEG potentials can be detected when participants listen passively after training (Bangert & Altenmüller, 2003). Changes in activation patterns throughout the course of training were reported. Initially a widespread additional activation was observed that became focussed on left sensorimotor cortex later in training, and on left central and right fronto-temporal regions (particularly C3 and F10 electrodes) after the full 10 weeks of training. The study was strengthened by the inclusion of a control non-musician group who underwent similar training but notes were randomly assigned to the keys each trial so that no specific sound-action mapping could be formed. This ‘no-map’ group did not demonstrate significant changes in activation pattern. An additional group, consisting of professional pianists also demonstrated frontal, temporal and central activation, but showed a different pattern from the training group. Interestingly, in pianists, the widespread activation was similar for purely motor and purely auditory tasks, suggesting that the same multimodal network was established in this highly trained group and activated regardless of whether one or both modalities are presented (Bangert & Altenmüller, 2003). Taken together these results suggest that specific, or at least consistent, sound-action associations are required in order to modulate oscillatory activity in auditory and motor regions. The current study seeks to investigate coupling of these regions using oscillatory coherence to examine networks representing auditory and motor coactivation.
In the current experiment, participants will undergo an adaptive piano training regime, and EEG will be recorded before and after training, while they listen to three types of auditory stimuli. The aim of the training is to successfully learn a limited range of sound-action mappings of piano tones. This study seeks to investigate whether audiomotor training leads to changes in functional connectivity that can be measured by EEG TRCoh during passive listening. This study uses a similar approach to the methods used in a MST study (Altenmüller et al., 2009), but restricts electrodes to sensorimotor regions of interest over left central, right central, fronto-central and parieto-central locations.

As an extension of previous audiomotor research, I hypothesise that functional connectivity for auditory tasks will increase after musical training, and the modulation may be detected using TRCoh measures. However, as hypothesised in the previous chapter, increased functional connectivity may occur specifically only when hearing notes that were included in the training regime. Alternatively, as discussed in the previous chapter, more general connectivity changes may be demonstrated, by additional increases in TRCoh post-training, for auditory tasks that include other musical notes or purely rhythmic stimuli.

### 4.2 Materials and Method

This chapter reports additional analysis of the data used in the previous chapters. Participant information and data collection procedures are summarised in brief here.

#### 4.2.1 Participants

Participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), and had no more than one year of formal musical training. Twenty participants commenced the training, but seven did not reach the performance criterion, and therefore did not complete the experiment. Therefore, data from 13 participants (8 male, 5 female; age $24.3 \pm 5.74$ years) were included in the analysis. All participants gave informed
consent and the experimental procedures have been approved by The University of Auckland Human Participants Ethics Committee.

4.2.2 Adaptive training paradigm

The aim of the training aspect of the experiment was for participants to acquire audiomotor mappings for piano tones. Participants were trained using interactive training software (see Bangert & Altenmüller, 2003 for further details). Three second long tone sequences consisting of notes between C5 – G5 were generated online using values for the parameters (a) number of notes; b) range of notes; c) note length range) that met the criteria for a particular level (smaller values for lower levels). These tone sequences were played to the participant, who was then to attempt to reproduce the sequence on a keyboard. Each session began at Level 1 (easiest) and participants had to progress beyond Level 6 to complete the training part of the experiment. Each trial started with the presentation of the sequence of notes, then a white keyboard icon appeared to indicate that participants must attempt to play what they have just heard. This icon turned red when 3 s passed, indicating to participants to stop playing, and then the wait screen appeared. Participants started each training trial when they were ready.

The software is adaptive; trials increase or decrease in difficulty level according to the participant’s accuracy in three aspects of performance: pitch, timing and dynamics. Levels stepped up, down, or stayed the same, depending on performance of previous trials. Each session was terminated when the participant’s performance curve was at exponential saturation (i.e. when they reached their maximal level and ceased moving up or down levels). Participants heard the usual sound feedback of the piano, but there was no explicit feedback as to the accuracy of their reproduction (although participants could infer how their performance was going depending on whether the next trial increased or decreased). There were no visual or verbal cues such as tone names, music notation, and after their right hand
was placed over the correct group of keys, participants had their hands shielded from view during the trials.

4.2.3 EEG procedure

EEG was recorded during two sessions in an electrically shielded, sound-attenuated room. The first session preceded training and participants returned for the second session after they had completed the training to the level required. The EEG sessions consisted of Rest, Audio, and Audiomotor blocks. The Audio block consisted of three conditions, randomised in presentation – (a) Audio-T: tone sequences generated using the same notes as heard in the training paradigm (C5-G5), (b) Audio-U: tone sequences generated using notes of lower pitch (C3-G3), (c) Audio-W: rhythmic sequences (woodblock). Therefore, there were a total of five conditions.

In Audio trials, participants were instructed to listen to these 3 s sequences and asked to keep still and relaxed. After an inter-stimulus interval (6 s) the next tone sequence was played. The stimuli were synthesized online by the same software as in the training procedure, and were presented at a constant level of difficulty (Level 6 from the training paradigm). During the Rest block, participants were instructed to sit still with arm relaxed, fixating on the centre of the screen. In the Audiomotor block, participants were asked to listen to a tone sequence (generated using the same notes as in the training paradigm, at Level 6) and were asked to playback the sequence (as in the training paradigm). Playback duration was constrained to 3 s with computer instructions. After a 6 s interval, the next trial began. Blocks were presented in a counterbalanced manner across participants, and in total there were 40 trials per condition. Stimuli were presented binaurally using etymotic earpieces (ER2; Etymotic Research Inc., Illinois, USA).
4.2.4 Electrophysiological recordings

EEG was recorded from the scalp using 128-channel Electrical Geodesics amplifiers and Ag/AgCl nets (Electrical Geodesics Inc., Eugene, OR, USA). Continuous EEG was sampled at 1000 Hz, with 0.1 – 100 Hz analogue bandpass filter. Electrode impedances were maintained at an acceptable level for this EGI system (<45 kΩ) and data was recorded with Cz as a reference.

EMG recordings were monitored from the EDC and FDS of the right arm using disposable electrodes (Biovision, Wehrheim, Germany) at a sampling rate of 1 KHz with a 10-500 Hz Bessel bandpass filter. Any passive listening trials with detected movement were discarded before analysis. In addition to the EMG monitoring, experimenters were able to view participants via a video monitor and did not observe any overt movement. Finally, participants self-reported understanding the instructions and that they did not move during trials. Despite these measures, it is acknowledged that there could have been small activation of other muscles that were not monitored.

4.2.5 Task-related coherence analysis

Data was re-referenced to a common average reference (Nunez et al., 1997). Although earlobe electrodes are commonly used as reference electrodes in coherence analysis literature, these may not be as suitable for audiomotor studies due to the auditory nature of the task (Gerloff et al., 2003). The trials were segmented 200ms prestimulus to 3000ms poststimulus. Any trial where EMG activity was detected by visual analysis was discarded (mean rejection rate 6%, range 0 - 40%). For each trial, five non-overlapping 512 ms samples were taken, and eye movements were detected from VEOG and HEOG channels using custom written software. Any epochs with eye artifacts were removed, resulting in an average of 182 epochs per condition (range 107 – 200 epochs). The epochs were subjected to a FFT. Coherence was
calculated for the two frequency bands of interest: alpha (8 -12 Hz) and beta (13-20 Hz). The
following equations were used for calculating coherence between pairs of electrodes – firstly
the linear dependency of two electrodes (with signals x and y) for a frequency (\( \lambda \)) is an
extension of Pearson’s correlation coefficient (Eq.1). The numerator denotes the cross-
spectrum of the two signals, the denominator denotes the autospectra of each signal.
Coherence is calculated by squaring the complex correlation coefficient, to give a number
within the range of 0 and 1.

\[
Coh_{xy}(\lambda) = \left| R_{xy}(\lambda) \right|^2 = \frac{|f_{xy}(\lambda)|^2}{f_{xx}(\lambda)f_{yy}(\lambda)}
\]  
(Equation 1)

Data were then submitted to a hyperbolic inverse tangent (tanh\(^{-1}\)) transformation on
individual task and rest files to normalise the data across the range of coherence values, as
variance for numbers close to the boundaries (0 and 1) have less variance than mid-range
values (Farmer, Bremner, Halliday, Rosenberg, & Stephens, 1993; Rosenberg, Amjad,
Breeze, Brillinger, & Halliday, 1989). Following the normalisation, task-related coherence
was calculated by subtracting rest from task coherence values after stabilising the variances:

\[
\text{tanh}^{-1} TRCoh_{xy} = \text{tanh}^{-1} Coh_{xy,\text{task}} - \text{tanh}^{-1} Coh_{xy,\text{rest}}
\]  
(Equation 2)

The subtractive nature of this method helps to minimise variability between subjects and
electrode pairs, as well as reduce volume conduction issues (Cassidy & Brown, 2001; Gerloff
et al., 2006). Furthermore, due to this subtraction, any bias from selection of reference
electrode is less likely to affect the data (Gerloff et al., 1998).

In order to assess training-related changes in coherence, 27 combinations of pairs of 9
electrodes of interest were selected, based on previous studies of sequential movements
(Gerloff et al., 1998; Manganotti et al., 1998). These included 9 pairs of left central to mesial
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frontocentral electrodes, 9 pairs of left central to right central electrodes, and 9 pairs of right central to mesial frontocentral electrodes Figure 4.2. The equivalent 10-10 electrode positions for the 128-channel EGI Hydrocel Geodesic Net were used (Figure 4.1).

*Figure 4.1* The 128-channel headmap depicting 10-10 electrode position equivalents. The nine electrodes of interest were equivalent to C3, FC3, CP3, Fz, FCz, Cz, C4, FC4 and CP4. Original map template provided by Electrical Geodesics, Inc.
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Wilcoxon (exact) signed-ranks tests were carried out for each of the 27 pairs of interest, to assess task-related changes between post and pre-training sessions (Altenmüller et al., 2009). Each condition (trained piano tones, untrained piano tones, rhythm) was studied separately. Coherence increases after training were of interest, and there was no a priori hypothesis for a decrease in TRCoh (Gerloff & Andres, 2002). Therefore, directional one-tailed tests were performed.

Figure 4.2 The 27 electrode pairs of interest. Original map templates provided by Electrical Geodesics, Inc.
4.3 Results

4.3.1 Training behaviour

Thirteen participants reached the required level in training. Training data is reported and discussed in the previous chapter.

4.3.2 EEG coherence

*Figure 4.3* shows pairs of electrodes that had a significant increase of beta coherence for two of the auditory (Audio_T and Audio_U) conditions. Left sensorimotor electrodes had greater coherence with right posterior and frontocentral electrodes after training. Specifically, for the Audio_T condition, this was seen in C3-FCz and for the Audio_U condition, in C3-FCz, C3-CP4, and CP3-CP4. In the alpha band, coherence significantly increased after training for Audio_U in CP3-FCz, but no electrode pairs showed an increase in TRCoh in Audio_T (Table 2). There were no significant increases in alpha and beta coherence found for the rhythm condition.

Table 2
*Task-related coherence for electrode pairs that were significantly different between pre-training and post-training.*

<table>
<thead>
<tr>
<th>Frequency Band</th>
<th>Condition</th>
<th>Electrode Pair</th>
<th>Mean Difference</th>
<th>SE</th>
<th>z</th>
<th>p-value (one-tailed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beta (13-20 Hz)</td>
<td>Audio_T</td>
<td>C3-FCz</td>
<td>0.03</td>
<td>0.029</td>
<td>-2.062</td>
<td>0.019</td>
</tr>
<tr>
<td></td>
<td>Audio_U</td>
<td>C3-FCz</td>
<td>0.01</td>
<td>0.02</td>
<td>-1.992</td>
<td>0.020</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C3-CP4</td>
<td>0.05</td>
<td>0.020</td>
<td>-2.062</td>
<td>0.024</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CP3-CP4</td>
<td>0.04</td>
<td>0.022</td>
<td>-1.782</td>
<td>0.040</td>
</tr>
<tr>
<td>Alpha (8-12 Hz)</td>
<td>Audio_U</td>
<td>CP3-FCz</td>
<td>0.05</td>
<td>0.020</td>
<td>-2.271</td>
<td>0.011</td>
</tr>
</tbody>
</table>
a) Beta band (13-20Hz) TRCoh:

b) Alpha band (8-12Hz) TRCoh:

Figure 4.3 These headmaps display the pairs of electrodes where TRCoh increased significantly post-training relative to pre-training: a) beta band TRCoh for Audio-T and Audio-U; b) alpha band TRCoh for Audio-U. Original map template provided by Electrical Geodesics, Inc.

4.4 Discussion

In this chapter, training-induced changes in cortico-cortical task-related coherence between electrodes that cover the sensorimotor network of regions were investigated. A
comparison between pre- and post-training revealed an increase in task-related coherence between specific electrode pairs post-training, in the two passive listening tasks which included piano tones as stimuli. Interestingly, the pattern for beta band TRCoh modulation is similar for the tasks that involved listening to piano tones, whereas there was a lack of increased TRCoh when a rhythmic sequence was heard, suggesting that the training effect could be specific for the type of sounds associated to action during training.

The results may appear to contradict the idea that the presence of any metrical structure is sufficient to engage an audiomotor network, because we inherently move to the beat (Chen et al., 2008, 2006; Kornysheva, Yves von Cramon, Jacobsen, & Schubotz, 2010). For example, in an fMRI study where rhythms were played to participants, it was found that when people expect to have to tap the rhythm back, an audiomotor network is activated, and musical training was not necessary (Chen et al., 2008).

However, this study focusses on changes in functional coupling due to musical training. If we consider that the audiomotor network is already engaged when hearing the rhythms prior to training, we should not see any change in rhythm-related coherence between pre- and post-training. Functional coupling, measured using coherence, may already occur prior to training, which would mask any training-related change. This would also suggest that coherence for pairs of electrodes for the rhythm condition would be different to pre-training piano tone conditions. Post-hoc Wilcoxon signed-rank tests comparing pre-training piano tone conditions with the rhythm condition did not reveal any significant effects. Therefore, even though our spontaneous urge to move to the beat may result in audiomotor coupling, learning specific sound-action mappings may further enhance or increase the integrative recruitment of multimodal regions of the brain.
CHAPTER 4: MUSICAL TRAINING AND EEG COHERENCE

Another fMRI study showed that premotor activity increased during preferred musical rhythms as opposed to beats that were not as appealing to the listener, suggesting that subjective factors may play an important role in the nature of the inherent motor response to hearing rhythmic sounds (Kornysheva et al., 2010). The woodblock rhythms were fairly simplistic in this experiment, and therefore perhaps not appealing or long enough to demonstrate the effects that the studies above reported. These rhythmic stimuli were used to match the rhythm of the learned sequences. Longer and more varied rhythmic sequences could be investigated in the future to explore this idea. Nevertheless, it can be concluded that sound-action mapping training did not result in increased functional connectivity in sensorimotor regions during the perception of simple rhythmic sequences.

An electrode over left sensorimotor cortex displayed increased coherence with a fronto-central electrode post-training for any piano notes heard – that is, not only for the notes that participants had learned in training. This suggests that the coherence effect is not specific to the particular sound-action mappings learned in training. However, as previously discussed, there is some degree of specificity of sound-action mapping, as listening to a woodblock playing similar rhythm sequences did not result in any change in coherence. Bangert & Altenmüller's (2003) sound-action mapping group demonstrated greater activation over the same left sensorimotor cortex (C3) than their ‘no-map’ group when listening to sequences. They also showed a frontotemporal increase in activation in the right hemisphere, which they speculate may add support to the notion that this area is involved in multimodal functioning. Coherence analysis was also performed on this data, and increased coherence between motor and auditory regions was reported, but no further details were discussed (Bangert, Haeusler, & Altenmüller, 2001). Therefore, similarity between results with the current study cannot be assessed.
Interestingly, the coherence analysis also revealed some cross-hemisphere coupling, although between more posterior electrodes. When the participants listened to sequences of notes which were not in the training sequences, the additional coupling was between left and right hemisphere electrodes. The untrained notes played to the participants were notes that were towards the left on the piano keyboard (lower in pitch) and would often be played by the left, rather than right hand. These participants have not been trained in playing the piano notes with the left hand, but one can speculate that hearing notes lower in the range may involve regions on the contralateral side to the left hand – the right hemisphere. The short amount of training, perhaps, was sufficient for participants to additionally learn a horizontal spatial mapping for pitch height, a type of association that has been reported in pianists (Stewart, Walsh, & Frith, 2004). Alternatively, or additionally, there could be some transfer or generalisation of skill seen here, that occurs without training the left hand. In future studies, the training sessions could be extended to incorporate left hand training, to investigate these transfer and laterality effects.

There are some limitations of this study that require discussion. Based on previous literature, a pairs of interest analysis was performed, and these results cannot be extended to determine the exact anatomical source of the oscillatory coupling. However, the focus of this study was to determine if oscillatory coupling modulations did occur in sensorimotor regions after training, and the electrodes selected have been shown to represent sensorimotor activity (Andrew & Pfurtscheller, 1996). Statistically, as there are 27 pairs of interest, one must be aware of the potential issues with multiple comparisons and be cautious when interpreting results. However, the methods that were performed have been utilised in past research, and the two piano tone conditions revealed a similar pattern of increase with the main electrode being in the left hemisphere over sensorimotor cortex. These results are in accordance to findings that beta coherence has a role in functional connectivity between sensorimotor
regions, and C3 has robustly been shown as a site involved in sensorimotor activity (Andrew & Pfurtscheller, 1996; Bangert & Altenmüller, 2003; Manganotti et al., 1998). TRCoh modulations between this particular electrode and other sensorimotor electrodes is expected, given that the participants only learned sound-action associations with their right hand in the training phase. In addition, modulations in coherence were only revealed for specific pairings, and not every condition revealed significant effects. This also suggests that it is highly unlikely that volume conductance and selection of reference electrode effects are the only explanation for the increases in coherence seen after training. Despite these limitations the findings of the current experiment do suggest that TRCoh is a useful measure to investigate the coactivation of distinct areas. After participants learnt sound-action mappings by undergoing piano training, there was an increase in functional connectivity in sensorimotor regions during listening tasks that include piano tones but not generic rhythmic stimuli.

Understanding modulations in functional connectivity due to training through TRCoh methods is proving useful for a clinical application. To gain more insight into the process of functional reorganisation during stroke recovery, studies have utilized coherence analyses to demonstrate the effect of motor therapies (Hummel & Gerloff, 2006). More recently, in the music domain, oscillatory changes in coherence can measure functional plasticity that occurs when stroke patients undergo MST, compared to conventional motor recovery therapies (Altenmüller et al., 2009; Fujioka, Ween, Jamali, Stuss, & Ross, 2012). With this EEG method, further insight into oscillatory coupling changes that occur due to musical training can be gained. The current study adds to the evidence that after musical training, multimodal coupling occurs even in the absence of one of the modalities. With further research, perhaps a passive listening component could be incorporated as part of MST to enhance the audiomotor training, thereby minimizing muscle fatigue and maximizing therapeutic effects.
Chapter 5. General Discussion

5.1 Summary of Findings

The current thesis investigated the effects of musical training on audiomotor integration. By examining the EEG mu rhythm, audiomotor coupling effects were explored in musicians and non-musicians. Musicians are seen to have superior sensorimotor skills due to their training, and understanding the development of strong sound-to-action links in non-musicians may help to improve rehabilitation strategies.

Mu suppression had been shown previously in musicians during sheet music reading and viewing videos of music performance – tasks that involved a visual component (Behmer Jr. & Jantzen, 2011). In the first study (chapter two), these findings were extended to the audiomotor domain. Study 1 showed that musicians demonstrated mu suppression during passive listening to piano melodies. Only one type of listening stimulus (extracts of known melodies) was included, and therefore a comparison with unfamiliar auditory stimuli was unable to be made. However, the aim of this study was primarily to determine if a purely auditory stimulus would result in attenuation of the mu rhythm over sensorimotor cortex, providing a likely index of action representation. Musicians demonstrated an action representation response, which provided the foundation for the subsequent studies that included more than one type of auditory stimulus.

The second study (chapter three) investigated short-term audiomotor training and mu rhythm modulation in non-musicians. In Study 2, non-musicians learned to map specific sounds (piano tones) to particular actions (specific finger movements to press piano keys). The mu frequency band in EEG was recorded during passive listening tasks before training commenced, and after training was completed. We sought to determine if a post-training mu suppression effect occurred specifically for the trained sound-action associations, or whether
a rhythmic stimulus also produces a mu suppression effect. Three auditory stimuli were presented in the EEG sessions of this study: sequences that contained trained piano tones; piano tones that were different to the trained piano tones (two octaves lower than the trained tones); and woodblock sequences of rhythms similar to those encountered in training. This study did not find mu suppression effects for any of the types of stimuli after participants had acquired sound-action associations.

This study did, however, tangentially address an issue from the first study, as this non-musician group were presented more than one type of stimuli. Therefore, these data are not consistent with the notion that any stimulus can result in mu suppression in any participant, and provide support for the idea that action representation demonstrated by musicians can be indexed by mu rhythm desynchronisation. Mu suppression for passive listening was not revealed in non-musicians in the second study, suggesting that the musician group in the first study might have superior audiomotor integration, and that this is the key to finding mu suppression.

Study 3 (chapter four) aimed to elucidate the modulation of functional connectivity after short-term training. Greater functional connectivity was revealed when participants listened to sequences of piano sounds after training, but not when rhythms were heard. These increases in connectivity involved the left sensorimotor cortex, the side contralateral to the hand that performed the finger movements during training. The effect was also seen for sequences of piano notes other than those on which the participants trained. These effects were mainly seen within the beta frequency band of mu rhythm.

Taken together, the three studies may appear to contradict each other. The first showed action representation effects in musicians. The second did not find action representation effects in non-musicians after they had reached a certain level of proficiency in piano sound
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to finger press coupling (that enabled them to reproduce a randomised sequence of trained notes.) Nevertheless, the third study revealed increased functional connectivity after training in the non-musicians.

However, the studies differ from one another, as each sought to address specific research questions. For Study 1, the audiomotor sequences presented were melodies that had been rehearsed by the musicians as part of their learned repertoire. These stimuli were similar to that in a previous audiomotor coupling training study, which was a major basis of this thesis (Lahav et al., 2007). In their study, non-musicians were trained to play a complete musical piece. In other words, both of these studies used audiomotor sequences known to the participants.

In Study 2, participants were presented with randomised melodies because the intention was to have them map specific but abstract sound-actions. Furthermore, rather than investigating sequence effects, the intention here was to focus on the sound-action association. Therefore the musicians in Study 1 and non-musicians in Study 2 listened to different types stimuli. In hindsight, it might have been interesting to play randomised melodies to musicians as well, although these combinations of notes would have most probably been familiar sequences to the highly skilled pianists who constituted this group in Study 1.

Study 3 comprises of the same group of non-musicians and same stimuli, but focused on the connectivity between regions, as opposed to regional activation. Oscillatory coherence effects are not necessarily accompanied by similar modulations of regional oscillatory activity (Gerloff et al., 1998; Manganotti et al., 1998; Pfurtscheller & Andrew, 1999). For example, Gerloff and colleagues (1998) suggested that inter-regional coupling could be modulated in motor tasks without accompanying changes in regional activation. Their
comparison between internally and externally paced movements revealed differences between tasks in beta coherence but not beta power.

A similar differentiation between the modulation of inter-regional connectivity and regional activation was reported during beat perception in an fMRI study (Grahn & Rowe, 2009). Psychophysiological interaction analyses revealed greater coupling between SMA, PMC and auditory cortex when musicians listened to rhythms, compared to non-musicians, but activation in those regions of interest did not parallel these group differences.

An alternative explanation for finding post-training effects of functional connectivity but no regional activation effects, could be that activation and connectivity modulations show differential effects at different stages of audiomotor skill acquisition. These could relate to the varying stages found in the motor learning literature. For example, Halsband and Lange (2006) outline motor learning from trial and error phase to rapid and automised reproduction in three phases: an initial, intermediate, and advanced stage. They report that these stages are apparent in learning behaviour as well as the involvement of varying neural activation patterns (see Halsband & Lange, 2006 for review). In Bangert and Altenmüller’s (2003) passive listening task, the activation pattern measured mid-training was diffuse, before becoming more focal over left sensorimotor cortex after training was complete. One could speculate that this parallels a potential increase in coherence between regions mid-training, that precedes a modulation of regional oscillatory activation, which occurs after completion of training. The training procedure used in Study 2 and 3 proved to be difficult for non-musician participants. This may indicate that sound-action mappings were still in the process of being acquired and had not reached the more focal activation stage that Bangert and Altenmüller’s (2003) group had reached by the end of training. During initial learning, widespread regions may become more synchronised but only after an intermediate stage of learning, a change in the regional oscillatory activation will be detected. The musicians in
their study may be at a further advanced motor learning stage (stage three according to Halsband and Lange (2006)), that has achieved even greater automaticity and motor adaptation skill, explaining why their pattern of cortical DC-potentials differed from the trained non-musicians. Similarly, the musicians in Study 1 of this thesis, who demonstrated action representation effects as indexed by mu suppression, would also be advanced in motor learning.

Furthermore, the alpha frequency band of the mu rhythm was investigated in Study 1 and 2, due to those studies being based on visuomotor studies that examined the same frequency band (Muthukumaraswamy et al., 2004; Pineda, 2005; Pineda et al., 2013). Coherence was investigated in both alpha and beta bands as beta coherence has been discussed in the literature in terms of audiomotor integration and functional coupling (Altenmüller et al., 2009; Andres & Gerloff, 1999; Classen, Gerloff, et al., 1998).

These discrepancies were purposefully built into the research design of the thesis due to their use in the previous research literature informing each study. It would be of interest to extend Study 1 to determine if mu suppression effects in beta frequency band may differ from the alpha frequency band. In addition, in order to make further comparisons with other brain imaging methods, the current studies could be expanded by using source estimation methods. The current thesis uses electrode locations over sensorimotor cortices, in which the mu rhythm has been found to be maximal. However, source localisation techniques could add considerable further insight, especially for the oscillatory coherence study, where one might investigate coherence reconstructed from identified sources. Source analyses might also identify other regions of interest that may become coupled through the acquisition of sound-action associations.
5.2 The Training Phase

Perhaps the most surprising outcome from this thesis was observed during the training procedure undertaken by the non-musicians. Many participants required longer than the set time to reach the performance criterion. Furthermore, seven out of the 20 participants did not learn to reproduce the randomised sequences of notes to the prescribed level of proficiency and therefore could not complete the experiment. Randomised sequences were used so that each piano tone mapped to a specific finger press of a piano key. Learning these randomised stimuli may not have been very rewarding, which may be an explanation for the slower rate of learning than expected. Furthermore, randomised sequences may have been difficult for some participants, which could also result in poor motivation. Learning a simple musical piece, however, might have made the training phase more motivating for participants, and therefore more successful. Apart from Bangert and Altenmüller’s (2003) study, other training studies have consisted of learning either set piano pieces (Engel et al., 2012, 2014; Lahav et al., 2007) or musical scales (Baumann et al., 2007), i.e. learned audiomotor sequences. One other study did present random sequences of trained notes but in a very basic rhythm (notes of equal duration) (Chen et al., 2012). Moreover, Chen and colleagues designed their paradigm so that participants learned set melodies in the first part of training, followed by the random sequences that were presented as the second part of training. These studies suggest there may be fundamental difference between learned audiomotor sequences and the individual sound-action associations that are drawn upon when hearing randomised sequences. Furthermore, one might speculate that hearing a learned audiomotor sequence is similar to observing a goal-directed action, which may affect the action representation response indexed by mu suppression (Muthukumaraswamy et al., 2004). If randomised sequences are likened more to non-goal-directed actions, less mu suppression would be expected.
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The training phase was not expected to be such a challenge, as it was based on the adaptive training paradigm used in a previous study (Bangert & Altenmüller, 2003). This previous study reported that participants learned to reproduce the randomised sequences of notes to a higher performance criterion than Study 2. Furthermore, their training phase consisted of fewer sessions than Study 2’s originally prescribed 15 sessions. This points to a group difference between the non-musicians who participated in the current thesis and Bangert and Altenmüller’s (2003) study.

The integration of pitch with rhythm during the acquisition of sound-action associations adds complexity to the audiomotor coupling process, and highlights the complex nature of music performance. The reason for setting the performance criterion to a level where the rhythm was more complex than an even duration of notes, was to create a more salient rhythm in the woodblock stimulus. A sequence of five equal duration notes may not be as rhythmically salient as a five note sequence that incorporates a change in duration of one note (resulting in a ‘duration beat’). This was required, in order to investigate audiomotor response to rhythmic stimuli; however, having a more complex sequence could have profoundly contributed to the difficulties participants had with reaching adequate performance level. As an aside, this reminds us that a very high skill level is required to be proficient at music performance.

These issues that arose from the training phase of Study 2 and 3 may have contributed to the lack of effects with respect to mu desynchronisation in particular. However, training outcomes potentially add insight – training behaviour is important to investigate as it influences the findings of sensorimotor training studies. Furthermore, individuals train at different rates and may use different strategies of learning, as highlighted in two recent reviews (Herholz & Zatorre, 2012; Paraskevopoulos & Herholz, 2013). They emphasise that individual differences should be addressed in future directions of multimodal integration.
research. One method that partially addresses these differences is to categorise participants as good versus poor learners, using behavioural performance measures. An oscillatory coherence study has utilized this method for a multimodal tracking task, where only good learners were included in the examination of (non-music) visuomotor and audiomotor tracking tasks (Blum et al., 2007). Another study that made this categorical distinction showed that strong learners in a pitch memory task showed markedly increased activation in supramarginal gyrus (and a trend in Heschl’s gyrus) than weak learners (Gaab, Gaser, & Schlaug, 2006). In the field of sensorimotor integration and musical training, individual differences have recently been correlated to white matter integrity of tracts involved in sensorimotor processes (Engel et al., 2014). This study suggests that differences in training ability could arise from structural variations; however, there was no difference in structure (as measured by voxel-based morphometry) or function (activation during the pre-training pitch memory task) of strong learners compared to weak learners in the pitch memory study (Gaab et al., 2006). This suggests that individual differences cannot necessarily be predicted prior to administering training procedures.

One issue that arises when addressing individual differences is that poor learners may not reach specified performance criteria, and subsequently, as Blum and colleagues (2007) report, they cannot always be included in investigations of learning-related effects. Furthermore, weaker learners may be unable to perform post-training tasks proficiently and therefore, again cannot be included in the final analyses, as is the case in the current thesis. Nevertheless, one must carefully take into consideration the degree of difficulty of the training, that different strategies may suit different individuals and that individuals with varying learning abilities may demonstrate differing responses in brain activation and connectivity.
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5.3 Applications of Audiomotor Research and Future Clinical Directions: Music-Supported Therapy

Recent reviews have also highlighted the development of rehabilitation techniques as a direction for future research, and already there are treatment strategies that involve sensorimotor networks and musical training (Aglioti & Pazzaglia, 2010; Altenmüller & Schlaug, 2013; Herholz & Zatorre, 2012). Coupling of sensory and motor areas may be increased through learning to play a musical instrument. This sensorimotor training may lead to plastic changes in the brain, and may enhance standard motor rehabilitation strategies. MST consists of rehabilitation sessions using a piano keyboard and/or drum pads, both of which produce piano sounds (Schneider et al., 2007). Having two types of instruments gives the advantage of targeting either larger muscle groups for drumming, or finer finger movements, for those patients who are able to use the piano keyboard; i.e. the specifics of the training protocol are flexible and dependent on an individual’s symptoms. Patients attempt to reproduce sequences played by the therapist, for multiple 30 minute sessions during a 3 – 5 week training procedure. Initial studies have documented promising clinical improvements from MST (Schneider et al., 2010, 2007). Recent studies are beginning to elucidate changes in brain activation and connectivity as potential explanations for the therapeutic effects.

MST introduces sensory feedback to accompany the repetitive motor training aspect of rehabilitation. This involvement of sensory, in particular auditory, feedback is related to the sensorimotor integration that results in action representation for sounds. Indeed, a series of preliminary fMRI findings have been outlined that include strengthened functional connectivity in audiomotor networks during music listening after MST (Rodriguez-Fornells et al., 2012). It has been suggested that the clinical improvements are a result of both the sound-action associations created during training through premotor cortex mirror neurons, and a broader, more general mechanism of rhythmic and beat perception activating motor
networks. Rodriguez-Fornells and colleagues (2012) also suggest that the beat information facilitates the functional change in the audiomotor network. Action representation for rhythmic listening may be the underlying foundation for action representation for specific sound-action associations to be formed.

MST studies have utilised oscillatory measures in the investigation of neural activation and connectivity changes. Training-induced modulations in neuromagnetic beta band power were reported for three stroke patients who underwent MST (Fujioka et al., 2012). Motor improvements were minimal, but may have required a longer intervention time for greater behavioural outcomes than the 5 weeks undertaken. Furthermore, poststroke onsets of these patients were > 1 year, and it is suggested that earlier intervention is more effective. An early MST study revealed greater motor improvements in acute stroke patients than a subsequent study with chronic patients (Amengual et al., 2013; Schneider et al., 2010). Nevertheless, these studies hint at the potential positive effects of MST as oscillatory activity has been shown to be modulated even in chronic patients. EEG oscillatory changes in activity and connectivity have also been reported and suggest that MST leads to neural changes underlying the clinical effects (Altenmüller et al., 2009). Improvements in corticoexcitability have also been reported in a TMS study, as indexed by increased MEPs measured from the affected side post-training (Amengual et al., 2013). Further studies using these various methods will enable a more detailed understanding of the structural and functional changes in, and the potential beneficial effects of, MST.

Action representation studies may be able to contribute to incorporating sensory-only sessions as part of the rehabilitation training or testing. Active music-making is required to form sensorimotor coupling, but patients may have more tolerance for longer or more frequent sessions, if some included only listening to music and therefore may reduce potentially limiting restrictions due to muscle fatigue. Furthermore these non-performance
sessions could take the form of audiovisual (or audio and visual) trials that can be carried out without a therapist present. Moreover, the issue of accounting for individual differences is fundamental in developing rehabilitation strategies, and can be complicated by the extent and location of lesions and other individual health issues. Action representation studies could also contribute to MST research as the imaging methods utilised in the above studies might provide measures that can help predict recovery and aid how therapy may need to be adapted during the course of rehabilitation.

It must be acknowledged that as well as sensorimotor integration benefits, musical training has unrelated properties, such as motivational drive and enjoyment factors, that lends itself well to contributing to the effectiveness of treatment (Rodriguez-Fornells et al., 2012). These are crucial properties that may need to be teased apart from audiomotor integration effects; however, investigating the interaction between these properties and the strengthening of sensory and motor neural networks through musical training could contribute to refining rehabilitation methodology.

5.3.1 Building the blocks of sensorimotor integration for rehabilitation

The results from the current thesis suggest that rehabilitation strategies may be improved by incrementally increasing the complexity of sensorimotor stimuli. It appears that rhythm and beat perception can have an important role in sensorimotor training. Perhaps, rehabilitation could be approached in a way that gradually incorporates aspects of sensorimotor integration systems in a series of training ‘building blocks’. These could begin with basic rhythm synchronisation training, and move towards listening and initially, rhythm-only reproducibility tasks. In subsequent sessions, reproducibility of the pitch could be introduced, with training focussing on a set of specific melodies. Ultimately, this could be extended to randomised sequences. This type of approach would allow for adjustments to be
made in accordance with an individual’s own training progress. Functional activity and connectivity could be measured throughout the training process to add to behavioural measures and aid in adapting subsequent training.

5.4 General Future Directions and Conclusion

The specificity of the action representation response for music-related sounds was a fundamental topic of this thesis. Although in Study 2 non-musicians did not demonstrate the mu desynchronisation effects after musical training that musicians showed in Study 1, connectivity analysis in Study 3 did demonstrate significant changes after training. The oscillatory coherence effects that were revealed suggest that there is some degree of specificity towards the type of sound (piano) that was encountered during training, as a rhythmic stimulus did not reveal post-training modulation. It may be that oscillatory coherence is more sensitive in general, or perhaps more suited to detect modulation at the level of proficiency achieved in the training procedure used in this thesis.

This thesis drew from fields of multimodal processes, musical training, EEG oscillatory modulation and mirror neuron research. Directions of future research have been highlighted throughout this discussion. With the current thesis, more avenues could be explored in data analysis to include source estimation methods. Regardless of the unclear findings, this thesis still demonstrates that using music-related stimuli and musical training protocols can be beneficial for sensorimotor integration research.

Rehabilitation such as MST demonstrates the exciting directions that sensorimotor integration and action representation research can head towards. However, the current thesis highlights that training procedures can markedly influence the outcomes of research. Comparisons between types of sensorimotor training using musical stimuli can be studied.
using the wealth of brain imaging methods now available, and future research can combine this type of research with investigation into individual training differences.
Appendix

Melody extracts used as stimuli in Study 1 (chapter one).

JS Bach – Musette in D

JS Bach – Two-part Invention in F

Mozart – Sonata in C 1st movement

Schubert – Impromptu D.899 Op.90/1

Beethoven – Für Elise

Debussy – The Little Shepherd

Ravel – Sonatine 2nd movement

Kabalevsky - Clowns
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